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SKELETON AND MUSCULATURE OF THE HEAD OF *GELASTOCORIS OCULATUS* (FABRICIUS) (HEMIPTERA-HETEROPTERA)

BY MARGARET C. PARSONS

Harvard Biological Laboratories

CAMBRIDGE, MASS., U.S.A.

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No. 1 — *Skeleton and Musculature of the Head of Gelastocoris oculatus (Fabricius) (Hemiptera-Heteroptera)*

By Margaret C. Parsons
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INTRODUCTION

The family Gelastocoridae contains two genera, *Gelastocoris* and *Nerthra*. Its representatives are littoral, living in swamps or along the shores of ponds and streams, where they frequently burrow into the damp sand or mud. They are predaceous, feeding mainly upon other insects. Their prominent, laterally projecting compound eyes, their jerky, hopping means of locomotion, and their dark-colored, roughened exoskeleton have earned them the common name of "toad bugs."

Very little is known about the anatomy of gelastocorids. Earlier studies on the systematics of the Heteroptera have mentioned some of the more obvious features of their external anatomy, such as their possession of ocelli and short antennae. Hungerford (1922) studied the life history of *Gelastocoris oculatus* and made a few ecological observations on this species. In his extensive

study of the head capsule of the Hemiptera, Spooner (1938) discussed briefly the external appearance of the head of *Gelastocoris* sp. Todd (1955) made a taxonomic study of the family, describing the genitalia and some of the features of the exoskeleton. The presence of cephalic glands in *G. oculatus* has been reported (Parsons, in press), but, to the author's knowledge, almost nothing else is known of the internal anatomy of the Gelastocoridae.

The phylogentic position of the family is somewhat uncertain. It is generally believed that the aquatic Heteroptera arose from terrestrial forms, and most workers consider the shore-dwelling families to represent an intermediate stage in the progression from land to water. But whether the gelastocorids are more closely related to the totally aquatic Hydrocorisae or to the semi-aquatic Amphibicorisae is not generally agreed upon. Spooner (1938) placed them in the Amphibicorisae; China (1955b), however, considers them to be early offshoots of the ancestral Hydrocorisae. Since most of the theories presented by earlier workers have been based upon external anatomy alone, it appears that a study of the internal structure of a gelastocorid would be of value. The chief purpose of the present study is to present additional morphological evidence which might link the gelastocorids more definitely with either the Hydrocorisae or the Amphibicorisae. Although this paper is limited to the musculature and sclerotized parts of the gelastocorid head, the author plans in the future to extend the study to other systems and other parts of the body.

The literature on the hemipterous head is both extensive and confusing. One source of confusion is the variety of different terms which have been used for many of the structures. Another problem is that very few investigators have adequately described the complex relationships between the various endoskeletal elements. In the present study, an attempt has been made to bring together, wherever possible, the different terms which have been used for each structure, and to show how the various parts of the endoskeleton are interrelated.

I am grateful to the members of the C. V. Riley Entomological Society, of Columbia, Missouri, who supplied the live and preserved specimens used in this study. I also wish to thank Mr.

Edwin P. Marks of Washburn University for his helpful suggestions with regard to the gelastocorid food pump, and my husband, Dr. Thomas S. Parsons of Harvard University, for his advice and help with the preparation of the manuscript. This study was carried out during the tenure of the Ellen C. Sabin Fellowship, awarded by the American Association of University Women.

MATERIALS AND METHODS

Most of the observations were made on insects preserved in alcoholic Bouin's solution and stored in 70% alcohol. In order to have fresh material available when needed, live *Gelastocoris* were kept in the laboratory. They were placed in several large aquaria, allowing approximately 8 to 10 square inches of surface area per insect. The bottoms of the aquaria were filled with fairly coarse sand, which was kept moist at all times; the insects died if left without moisture for more than an hour. The bugs were fed vestigial-winged *Drosophila,* which were supplied in large numbers in order to discourage cannibalism. Cheesecloth coverings were placed over the tops of the aquaria to prevent the escape of the *Drosophila;* the gelastocorids were never observed to fly, or to climb more than a few inches up the sides of the aquaria.

In the microdissections of the heads, the techniques of Marks (1958 and 1959) were employed. The sclerotized structures were studied in heads which had been left in a hot concentrated solution of potassium hydroxide for approximately half an hour: this dissolved away most of the soft tissues. They were then dissected in glycerine or in 70% alcohol, under a stereoscopic microscope. The position of the frontal ganglion was determined by dissection (in 70% alcohol) of whole heads or of ones which had been cut parasagittally with a razor blade. In the larger of the two pieces thus obtained, the brain and frontal ganglion connectives were first located, and the latter were then traced to the frontal ganglion. The nervous and muscular tissues were clarified by introducing, with a fine pipette, a drop of Delafield's hematoxylin onto the surface of the dissection; this technique was suggested by Mr. R. B. Willey, of Harvard University.

Transverse, sagittal, and frontal serial sections were made through the heads of two adults, seven fifth instar nymphs, and

one fourth instar nymph. One of the nymphs was fixed in Carnoy's fluid, while the rest were preserved in alcoholic Bouin's solution. The heads were prepared for sectioning according to the Peterfi technique, embedded in 60-62° Tissuemat, and sectioned at 7 μ. The slides were stained in either Mallory's triple connective-tissue stain or Delafield's hematoxylin and eosin.

EXTERNAL ANATOMY

Figure 1 shows the dorsal surface of the gelastocorid head. It is triangular in shape, with prominent, laterally-projecting compound eyes, and with two ocelli. Between the ocelli is a broad, U-shaped indentation, and two shorter grooves lie lateral to each ocellus. These indentations produce, on the inner surface of the cranium, ridges for muscle attachments. Anterior to them

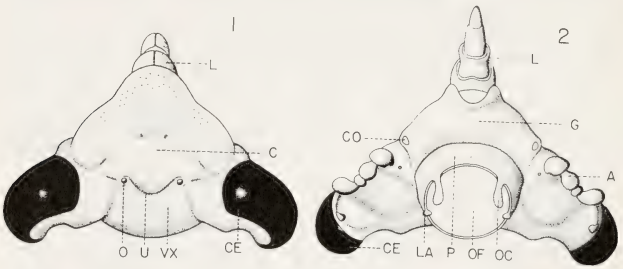


Figure 1. Dorsal view of the head. 14 X.

Figure 2. Ventral view of the head.

lie a pair of small pits, which mark the points at which the clypeal connectives (to be discussed later) contact the exoskeleton.

Although Spooner's (1938) diagram of the head of a *Gelastocoris* nymph shows an epicranial suture which forks in approximately the same position as the U-shaped indentation, neither the fifth instar nymphs nor the adults examined in the present study showed such a suture. Thus the boundaries of the facial sclerites are difficult to determine. According to Snodgrass

(1947), the medial facial sclerites can be distinguished by their muscle attachments; cibarial muscles originate on the clypeus and pharyngeal muscles on the frons. He further states that the forking of the ecdysial cleavage line (epicranial suture), which divides the frons from the vertex, occurs immediately above or behind the fronto-clypeal muscles. If Snodgrass' criteria, which have been employed by many workers, are followed here, the region of the head from the base of the labium to the U-shaped indentation may be termed the *clypeus* (*C*). As will be seen later, all the muscles originating in this area are anterior to the frontal ganglion, and are therefore cibarial. There is nothing to divide this region into an anteclypeus and a postclypeus, and lateral paraclypeal sutures are also absent.

The *frons* is much more difficult to define on the basis of muscle attachments. The anterior pharyngeal dilator muscles are reduced, in *Gelastocoris*, to only a few narrow strands (Fig. 27, *17 A*) which run between the brain and the frontal ganglion to attach to the U-shaped indentation. Also originating on this indentation, however, is a well-developed group of cibarial muscles (Fig. 27, *16*, *17*). Strictly speaking, therefore, the frons is limited to only a few small spots on the U-shaped indentation, while the rest of the indentation, like the region anterior to it, must be considered clypeal in nature. Rawat (1939) found a similar situation in *Naucoris*. Snodgrass' definition of the frons will be followed in the present study, although with some reservations. DuPorte (1946) has criticized Snodgrass' use of muscle attachments for the identification of sclerites, and it may be that the indentation and the region anterior to it should be termed the "fronto-clypeus."

The *vertex* (*VX*) is the region behind the U-shaped indentation. Spooner (1938) termed this the "frons" in adult gelastocorids; however, since none of the dilator muscles of the food pump attach to it, his term is incorrect.

A ventral view of the head (Fig. 2) shows the short, four-segmented antennae which lie beneath the compound eyes. The exoskeleton at the base of each eye is indented to receive the knob-shaped terminal segment of the antenna. Just anterior to the antennal bases, and situated on slight protuberances, lie the external *orifices of the cephalic glands* (*CO*); these have been

described in an earlier paper (Parsons, in press). The large *occipital foramen* (*OF*) is encircled by a collar-like rim of exoskeleton, which shall be termed, for convenience, the *postocciput* (*P*), although there is no definite suture separating it from the rest of the cranium. Ventrolaterally, it bears a pair of *occipital condyles* (*OC*) which project into the prothorax, and just dorsal to these is a pair of shorter *lateral apodemes* (*LA*). The ventral exoskeletal plate of the head is usually termed the *gula* (*G*) in the Heteroptera, and that term shall be used here. In *Gelastocoris,* the anterior edge of the gula is notched to allow the labium to swing downwards.

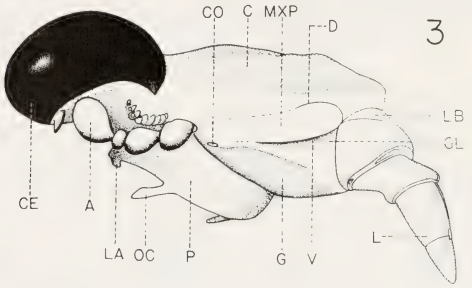


Figure 3. Lateral view of the head.

The only definite sutures on the cranium occur at its sides (Fig. 3). Extending anteriorly from the anterior border of the cephalic gland orifice to the lateral corner of the labrum is a fairly well defined suture. At the corner of the labrum it curves dorsally and then turns posteriorly to run to the posterior border of the glandular orifice. The dorsal part of this suture shall be termed the *dorsal suture* (*D*), and the ventral part the *ventral suture* (*V*). In adults, the dorsal suture is usually visible for only the anterior third of its length, but it may be seen in its entirety in fifth instar nymphs. The side of the head is quite flat, and forms rather sharp angles with the dorsal and ventral surfaces of the cranium. The sutures divide this flattened lateral

region into three general areas, a central one which is surrounded by the sutures (Fig. 3, *MXP*), a dorsal one (Fig. 3, *C*), and a ventral one (Fig. 3, *GL*).

The region above the dorsal suture appears to be a continuation of the clypeus, since, as will be seen later, the epipharynx is an inflection of its margins along the dorsal suture. Of the two remaining regions, Spooner (1938) has termed the central element the "paraclypeus" and the ventral one the "maxillary plate." The external topography of this region makes Spooner's interpretation seem quite plausible. In the majority of Heteroptera studied by that author, two sclerites are found in the lateral region of the head, a dorsal (or posterior) *paraclypeus* and a ventral (or anterior) *maxillary plate*. Typically the latter fuses with the gular area without a suture, thus resembling the region labelled *GL* in Figure 3.

Spooner's interpretation, which is based upon external appearances alone, is shown to be incorrect after examination of the internal structure of the head. One argument against his idea concerns the position of the mandibular lever. Other workers appear to agree that this lever is articulated to the cranium at the genal suture, which divides the more dorsal sclerite (the paraclypeus of Spooner, 1938; "lorum" of Hamilton, 1931, Butt, 1943, and Sprague, 1956; "jugum" of Snodgrass, 1935; "mandibular plate" of Griffith, 1945, and Akbar, 1957; "lamina mandibularis" of Benwitz, 1956; and "fulcrum" of Barth, 1952) from the more ventral sclerite (the maxillary plate of Hamilton, 1931, Spooner, 1938, Butt, 1943, Griffith, 1945, Sprague, 1956, and Akbar, 1957; "processus maxillaris" of Becker, 1929; "maxillary sclerite" of Rawat, 1939; and "lamina maxillaris" of Barth, 1952, and Benwitz, 1956). In *Gelastocoris* the mandibular lever joins the exoskeleton at the dorsal suture, at the point where this suture becomes indistinct in adults (Figs. 4, 5, 12). It seems, therefore, that the dorsal suture represents the genal suture of other authors, and that the sclerite lying below it (between it and the ventral suture) is not the paraclypeus but the maxillary plate. As will be discussed later, the paraclypeus of *Gelastocoris* (termed the *lorum* in this study) is wholly inflected within the head, and, as in some aquatic Heteroptera, is not visible externally.

A second argument against Spooner's use of the term paraclypeus for the sclerite here termed the maxillary plate is offered by the point of origin of the maxillary protractor muscles. Previous investigations all seem to indicate that the maxillary protractors originate on the maxillary plate or on an internal extension of this sclerite. In *Gelastocoris* these muscles originate on the anterior wall of the genal sac (to be discussed later), a pouch formed by marginal inflections of the sclerite which is enclosed by the dorsal and ventral sutures. This sclerite must, therefore, represent the maxillary plate. The area ventral to it, which Spooner termed the maxillary plate, is not separated from the gula in any way, and seems to be merely an anterolateral triangular extension of that exoskeletal zone. For convenience, it will be termed the *gular lobe* (*GL*).

At the base of the compound eye, lying just dorsal to the second segment of the antenna, is a peculiar curved ridge composed of numerous small tubercles (Fig. 3). A second, tooth-like protuberance is found at the ventromedial margin of the compound eye, just beyond the apical segment of the antenna (Figs. 2, 3). Whether these two protuberances have any special function is not known. The surface of the cranial exoskeleton is fairly smooth on the sides of the head, but the dorsal and ventral regions are covered with small tubercles giving them a roughened texture. Along the ventrolateral edge, the anterior dorsolateral edge, and the margins of the compound eyes are numerous long hairs (not shown in the figures), and finer, shorter hairs are scattered over the entire surface of the head, particularly on the antennae. Grains of sand cling to these hairs, and, along with the gray or brown color of the insect, produce an excellent camouflaging effect against sandy or muddy backgrounds.

The *labium* (Figs. 2, 3, *L*) is four-segmented and normally projects ventrally from the anteriormost part of the head. The dorsal part of each segment is invaginated to form the *stylet groove* (*SG*), which contains the apical parts of the four stylets (the *stylet bundle*). Lying across the posterior part of the basal segment is a broad, short *labrum* (*LB*) which is attached by a membrane to the anterior margin of the clypeus. It extends laterally as far as the edges of the maxillary plates.

INTERNAL ANATOMY

General Structure

Figure 4 shows a ventral view of the head after the removal of most of the exoskeleton. Anteriorly, the most ventral endoskeletal element is the broad, flat *suspensory plate* (*SU*). This extends anteriorly to the base of the labium; laterally it attaches to the dorsal border of the gular lobe, along the ventral suture. Along its posterior margin it is continuous with the right and left *ventral walls of the genal sacs* (*VG*). The *genal sacs* are paired pouches lying immediately dorsal to the suspensory plate; they are formed from inflections of the dorsal, ventral, and anterior margins of the maxillary plate. Dorsal to the genal sacs and extending posteriorly along the midline of the head is the *food pump* (*F*). On either side of the food pump are the two trough-shaped *hypopharyngeal wings* (*DH* and *VH*), the ventral surfaces of which are visible in Figure 4. Ventrally these are continuous with the united posterior portions of the suspensory plate and ventral walls of the genal sacs. Along the posterior border of the suspensory plate, lying between the bases of the two hypopharyngeal wings, is the *salivary pump* (*S*). Finally, attached to the exoskeleton at the dorsal sutures on either side of the head, lie the triangular *mandibular levers* (*MDL*), whose medial corners articulate with the bases of the *mandibular stylets* (*MD*).

The more dorsal structures are shown in Figure 5. Here it may be seen that the anterior walls of the food pump diverge and pass laterally to join the exoskeleton at the dorsal suture, just anterior to the point of articulation of the mandibular lever. Of this lateral diversion, the limited portion which arises from the floor or hypopharyngeal part of the food pump is here termed the *lorum* (*LO*). Fused with the lorum and extending anteriorly from it is a broad plate which reaches to the anteroventral margin of the labrum. This is the *epipharyngeal plate* (*PL*), and forms the anterior portion of the roof or epipharyngeal part of the food pump. Just ventral to the epipharyngeal plate lie the *dorsal walls of the genal sacs* (*DG*). Posteriorly these dorsal walls are continuous with the anterior edge of the mandibular lever; along their anterior margins they are continuous with the ventral walls of the genal sacs (not shown in Fig. 5). The dorsal surface of

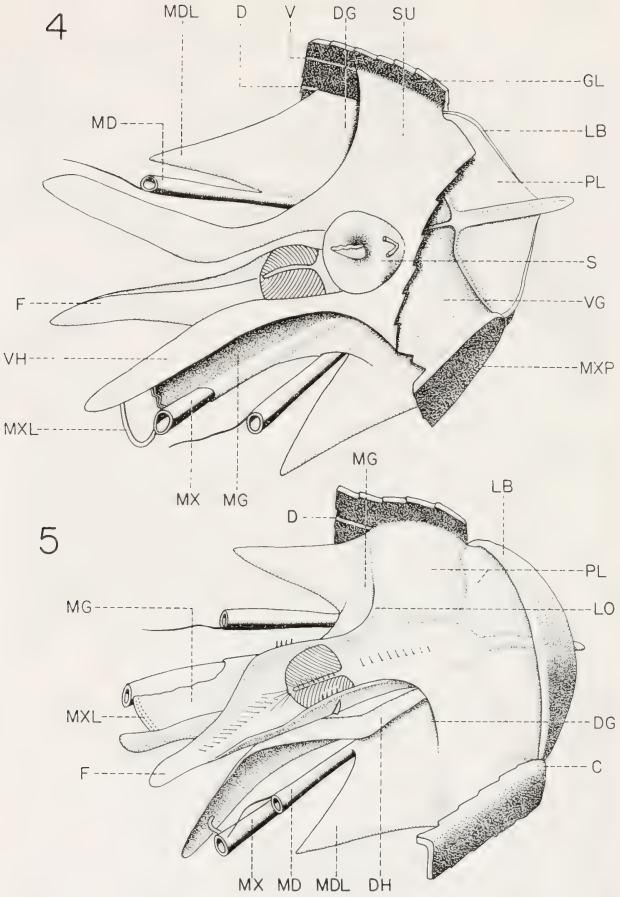


Figure 4. Ventral view of the endoskeletal structures after removal of most of the cranial exoskeleton. The right side has been tilted ventrally. Part of the suspensory plate has been cut away to reveal the genal sacs, and the posterior part of the medial wall of the genal sac (left side) has been cut off to reveal the maxillary lever. On the right side, the maxillary stylet and the medial wall of the genal sac are not shown. The labium and the stylet bundle are omitted.

Figure 5. Dorsal view of the endoskeletal structures after removal of most of the cranial exoskeleton. The right side has been tilted ventrally. The medial wall of the genal sac on the right side, along with the labium and the stylet bundle, are omitted.

the hypopharyngeal wing extends anteriorly between the epipharyngeal plate and the dorsal wall of the genal sac, and becomes continuous with the lorum and with the side of the anterior portion of the food pump (concealed, in Figure 5, by the epipharyngeal plate). Between the hypopharyngeal wing and the mandibular stylet lies the *maxillary stylet* (*MX*). A short, slender *maxillary lever* (*MXL*) connects its base with the tip of the hypopharyngeal wing. Extending between the maxillary stylet and the hypopharyngeal wing is a very delicate, thin double membrane, the *medial wall of the genal sac* (*MG*). In the anterior part of the head, this medial wall surrounds the stylets and the mandibular lever (Fig. 4, left side); posteriorly, its two lamellae enclose the maxillary lever.

Food Pump, Lora, and Epipharyngeal Plate

When the food pump is cut down the midline, as in Figure 6, its two-layered nature is revealed. The *hypopharynx* (*H*) (incorrectly termed the "anterior arms of the tentorium" by Hamilton, 1931), which forms the floor, and the *epipharynx* (*E*), or roof, lie close together, one upon the other. Transverse sections through the pump show it to be U- or V-shaped (Fig. 13, A-C). Posteriorly, the heavily sclerotized hypopharynx and the membranous epipharynx are joined along their dorsolateral margins, and a narrow cavity, the lumen of the pump, is thus enclosed between them. Anterior to the lora, however, the hypopharynx and epipharynx are not joined, although they are contiguous in the lateral part of the head (see Fig. 13D, right side).

The walls of the food pump are not, as in many Heteroptera, fused with the clypeus. Instead, the structure is held firmly in place by a few short, sclerotized connections, the *clypeal connectives* (*CN*), which run from the clypeus to the dorsolateral margins of the pump (Fig. 7). Anterior to these connectives, the pump is relatively broad, while posteriorly it gradually tapers to a narrow structure (Figs. 5, 9). A lateral view of the food pump (Figs. 6, 7) shows it to be somewhat arched, the region from the clypeal connectives to the lorum being raised above the anterior and posterior extremities.

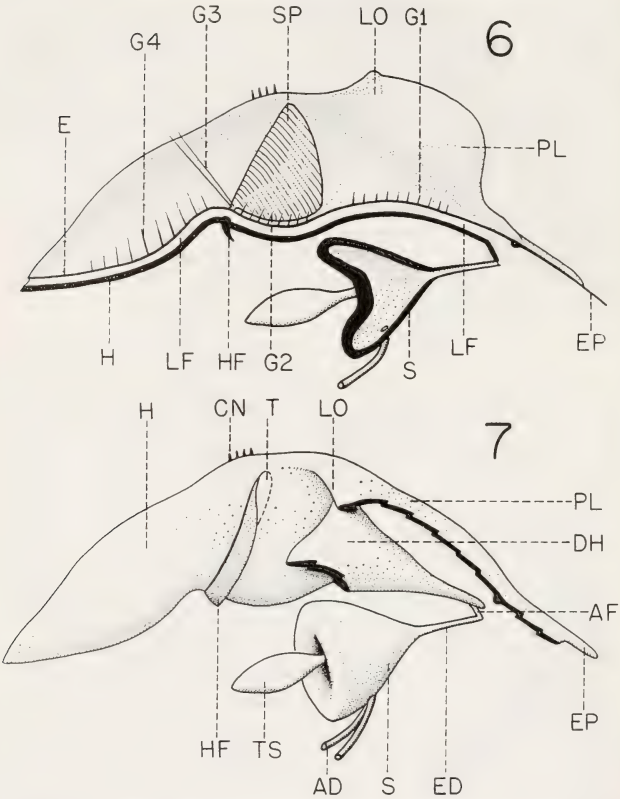


Figure 6. Lateral view of the inner surfaces of the left halves of the food and salivary pumps, after removal of the right halves. The anterior portion of the epipharyngeal plate is shown somewhat raised from its normal position.

Figure 7. Lateral view of the outer surfaces of the food and salivary pumps. The lateral portions of the lorum, epipharyngeal plate, and hypopharyngeal wing (dorsal surface) have been cut off.

The hypopharyngeal part of the pump is relatively simple. Just ventral to the clypeal connectives there is a slight transverse thickening in the hypopharyngeal wall. From this thickening a narrow, sclerotized *hypopharyngeal flap* (*HF*) extends anteriorly on the outer surface of the pump (Figs. 6, 7). Most of the hypopharyngeal wall directly in front of this flap is transparent, and thus there appears to be a break at this point. The hypopharynx is widest between this flap and the posterior edges of the lora; anterior to the latter, it tapers sharply (Fig. 8), forming a narrow trough (*AF*) which ends between the anterior borders of the genal sacs. Merged with either side of this narrow anterior trough lie the anteriormost extensions of the dorsal surfaces of the hypopharyngeal wings (Fig. 8); these are also continuous with the ventral surfaces of the lora of either side. They form a support for the anterior tip of the hypopharynx, and also, as will be discussed later, help to direct the path of the stylets in this region.

In most Heteroptera, those internal sclerotized structures which are here termed the lora are also visible externally. The external part of each lorum is a sclerite which, as was discussed earlier, has received many different names ("lorum," "paraclypeus," etc.). The internal extension of this sclerite, which is continuous with the hypopharynx of the food pump, has been termed the lorum (Snodgrass, 1938; Butt, 1943; and Akbar, 1957), the "mandibular plate" (Griffith, 1945), or the "lamina mandibularis" (Benwitz, 1956). Unfortunately, many authors have used the same term for both the external sclerite and the internal element, a practice which makes their descriptions somewhat confusing.

The lora of *Gelastocoris* appear to be contained entirely within the head, and there is no external sclerite present. It is difficult to determine the exact boundaries of the lora, since there appears to be considerable fusion between them and other structures. Laterally, they are partially fused with the underlying genal sacs. Dorsally, they join the posterior margin of the epipharyngeal plate, the line of fusion continuing the dorsolateral margins of the food pump (Fig. 8). Medially the epipharyngeal plate extends dorsal to the lora, while laterally it appears to come off from the anterior margins of the lora. According to Snodgrass

(1938), the lora are hypopharyngeal in nature. If this definition is used, the lora should be the parts which remain after the epipharyngeal plate is carefully torn off and after the walls of the genal sacs are pulled away from the hypopharynx. When this is done, the lora appear as in Figure 8; laterally they are very narrow, but they become somewhat broader medially where they join the hypopharyngeal walls of the food pump and the dorsal surfaces of the hypopharyngeal wings. The latter, which merge anteriorly with the sides of the food pump's floor, represent the anteriormost extensions of the lora. The anterior groups of mandibular protractor muscles (Fig. 26, *8*) originate on the posteromedial loral surfaces. In most specimens, the posterior

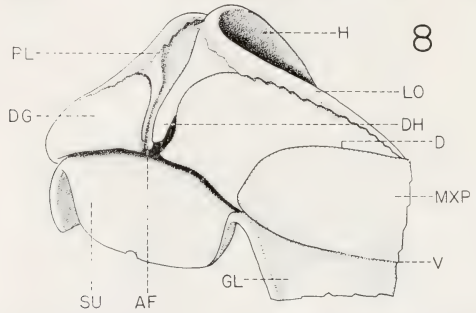


Figure 8. Anterolateral view of the food pump, lora, and genal sacs. The labium, labrum, clypeus, and most of the gula have been removed. The epipharynx has been removed from the hypopharynx, leaving a torn edge in those regions in which it was fused to the hypopharyngeal elements. The suspensory plate is bent ventrally, and the stylets are not shown.

edges of the lora are connected to the clypeus by a few short, sclerotized connectives, similar to the clypeal connectives of the food pump.

The epipharyngeal part of the food pump is somewhat more complex than the hypopharyngeal portion. Since the epipharynx is an inflection of the margins of the clypeus, it can be raised from the floor of the pump by separating the clypeus from the maxillary plate along the dorsal suture. Figure 9 shows the

ventral surface of the epipharynx after removal from the hypopharynx. Its posterior part is similar in shape to that of the floor of the pump. Most of its broad middle region, however, is modified to form a pair of roughly triangular, thickened plates (*SP*) which are joined posteriorly. The surfaces of these structures bear a series of regular, parallel striations, and they are, therefore, termed *striated plates* in the present study. Examination of a striated plate under a compound microscope reveals countless minute secondary ridges running at roughly 40 degree angles to these striations. At regular intervals along these secondary

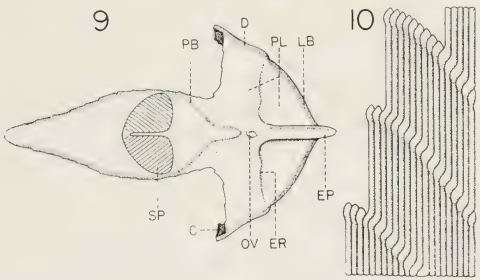


Figure 9. Ventral surface of the epipharynx after removal from the hypopharyngeal part of the food pump. The labrum and a small part of the clypeus are shown in place.

Figure 10. A marginal portion of a striated plate, as seen under the compound microscope. The thickenings in the narrow secondary ridges produce the striations which are visible in the dissections. Approx. 2000 X.

ridges are thickenings which lie side by side along adjacent ridges, thus forming the major striations (Fig. 10).

The margins of the posterior part of the epipharynx are strengthened by a well sclerotized, pigmented border. The latter extends anteriorly to a point approximately midway between the striated plates and the epipharyngeal plate, and then turns medially, disappearing along the midline of the epipharynx.

The epipharyngeal plate is continuous, along the dorsal suture, with the ventral margin of the clypeus (Figs. 5, 9, 12, 13E).

Anteriorly it is fused with the ventral surface of the labrum (Fig. 9). An anteromedial tongue-like projection of the epipharynx extends anteriorly a little beyond the labrum; this *epipharyngeal projection* (*EP*) helps to hold in place the stylet bundle, which lies directly ventral to it in the stylet groove of the first labial segment. For most of its length, the projection is somewhat concave ventrally. Its margins diverge laterally, just posterior to the base of the labrum, forming a transverse *epipharyngeal ridge* (Fig. 9, *ER*). This ridge probably represents the "Gaumenfalte" of Becker (1929); it lies just anterior to the anterior margins of the genal sacs, which underlie the epipharyngeal plate (Fig. 11). The stylets pass through the medial gap in the epipharyngeal ridge, which helps to direct them into the stylet groove of the labium.

Just posterior to the epipharyngeal ridge is an oval, sclerotized, raised area on the midventral surface of the epipharyngeal plate. This raised area lies just posterior to the point at which the efferent duct from the salivary pump opens onto the tip of the hypopharynx; its function may be to prevent the backflow of saliva into the food pump.

The muscles which operate the food pump insert by slender, sclerotized tendons projecting from the dorsal surface of the epipharynx along the midline. As shown in Figure 6, there are four groups of these processes, which shall here be termed Groups 1 through 4 respectively. *Group 1* (*G1*) extends from just posterior to the oval, sclerotized area to a point somewhat anterior to the striated plates. *Group 2* (*G2*) is located between the striated plates, while *Group 3* (*G3*) consists of only four or five very long processes attached to the joined posterior edges of the striated plates. Moderately long tendons make up *Group 4* (*G4*), which extends posteriorly from the striated plates, ending a short distance anterior to the posterior limit of the epipharynx. The muscles inserting by the tendons of Groups 1, 2, and 4 raise the roof of the pump, which snaps back into place elastically when the muscles relax; these movements create the pumping action of the food pump. The striated plates are moved back and forth in an anterior-posterior plane by the action of the muscles attaching onto Group 3; they are also raised and lowered by the

muscles of Group 2. These motions cause the highly ridged surfaces of the plates to rasp against the contents of the lumen of the pump. The author has noted no particulate matter in the gut of *Gelastocoris*, and the insect appears to ingest only fluids. It may be that the plates serve as straining or filtering devices, possibly breaking up small clots of material in the ingested fluid. Marks (1958 and 1959) has described somewhat similar epipharyngeal specializations in the food pumps of several fluid-feeding aquatic bugs, and interprets these as straining devices.

Salivary Pump

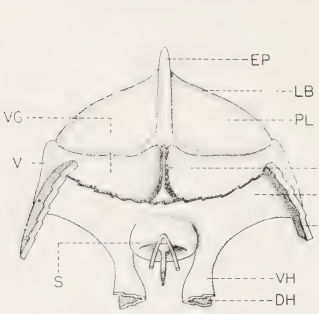
As seen in Figures 6 and 7, the salivary pump lies just ventral to the anterior half of the food pump. It is a large, bell-shaped structure, with a short, narrow *efferent duct* (*ED*) leading from its anterior end to open through the ventral surface of the hypopharyngeal tip of the food pump. Two slender *afferent ducts* (*AD*), which run from the salivary glands to the pump's ventral surface, convey the saliva to the lumen of the pump. The expanded posterior end of the salivary pump is invaginated, its walls becoming quite thickened. To the center of this thickened invaginated portion is attached a thin, plate-like tendon for the insertion of the salivary pump muscles. The latter enable the invaginated wall to act as a piston, which is pulled out by muscular contraction and springs back into place elastically when the muscles relax.

Hypopharyngeal Wings, Suspensory Plate, and Genal Sacs

The hypopharyngeal wings (Hamilton, 1931; Butt, 1943; Qadri, 1951; and Benwitz, 1956) have been variously termed the "posterior plates of the hypopharynx" (Snodgrass, 1938), the "sclerotized plates of the genal apodeme" (Rawat, 1939), the "maxillary sheaths" (Sprague, 1956), or the "ventral processes of the hypopharynx" (Akbar, 1957). Several authors, such as Ekblom (1926) and Becker (1929) mistook them for part of a tentorium. Whether or not a tentorium is present in the Heteroptera appears to be a disputed point; although Spooner (1938) and Butt (1943) deny its existence in heteropterans.

Akbar (1957) has described a remnant of a tentorium in the coreid *Leptocorisa*. The tentorium appears to be completely lacking in *Gelastocoris*.

As shown in Figure 5, the hypopharyngeal wings are plate-like processes on either side of the food pump. Transverse



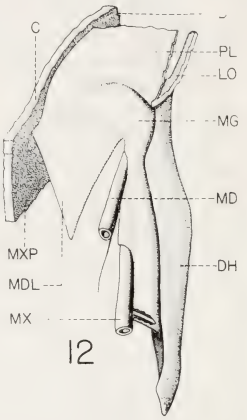


Figure 11. Ventral view of genal sacs, salivary pump, and associated structures. Most of the gula has been removed, and the gular lobes have been bent medially to show the ventral suture. The anterior part of the suspensory plate and the posterior portions of the hypopharyngeal wings have been removed. The stylets and the labium are not shown.

Figure 12. Dorsal view of the medial wall of the genal sac on the left side of the head. The anterior parts of all structures are cut off; the most medial portions of the epipharyngeal plate and lorum are cut away a little to the left of the midline. Posteriorly, part of one membrane of the medial wall has been removed to show the maxillary lever.

sections through the head (Fig. 13B) show that fine fibrillae (indicated by dotted lines) connect them with the walls of the food pump. The wings are folded along their longitudinal axes so that each is trough-shaped, divided by the medial fold into a *dorsal surface* (*DH*) and a *ventral surface* (*VH*). Dissections

of the hypopharyngeal wings reveal that they are actually two-layered; these layers can be separated anteriorly where the ventral surface contacts the exoskeleton, but posteriorly, in the trough-like portions, the two lamellae seem to be fused together, behaving as a single layer.

The anterior part of the dorsal surface of the wing has already been described. This surface extends directly anterior, becoming continuous with the ventral surface of the lorum (Figs. 12, 13D) and with the tip of the hypopharyngeal part of the food pump (Fig. 8). Anteriorly, the hypopharyngeal wing develops a series of longitudinal ridges and grooves (Fig. 13D). These act as tracks for the mandibular and maxillary stylets, and hold them in position.

The anterior modifications of the ventral surface of the hypopharyngeal wings are equally complex. Figure 4 shows that the lateral margin of the ventral surface diverges laterally to meet the exoskeleton along the ventral suture. If, in an undissected, potassium hydroxide-treated head, the gular lobe and the maxillary plate are separated from each other along the anterior part of the ventral suture, it may be seen that from this part of the suture an invagination arises. The invagination extends posteriorly to a point just below the place where the mandibular lever articulates with the dorsal suture. It produces two layers, a dorsal one and a ventral one, which extend medially into the head. Posteriorly, these lamellae are continuous with each other, and the line of fusion between them ("Querbalken" of Becker, 1929) is a continuation of the lateral edge of the ventral surface of the hypopharyngeal wing. Anteriorly, however, the two layers are entirely separate. The more ventral one, the suspensory plate, is continuous with the dorsal edge of the gular lobe, while the more dorsal layer, the ventral wall of the genal sac, is an inflection of the ventral margin of the maxillary plate (Fig. 13E).

The suspensory plate ("Aufhängeblatt" of Becker, 1929) extends from one side of the head to the other as a broad, single lamella. The posteromedial margin of this plate forms a bridge between the two hypopharyngeal wings, and extends across the ventral wall of the salivary pump, with which it is fused (Fig. 11). The suspensory plate extends anteriorly as far as the base of the first segment of the labium, with which it is partially or

completely fused. Laterally, it is bordered by the exoskeleton of the sides of the head. The medial part of its anterior edge forms a trough which is a posterior continuation of the stylet groove of the labium (Fig. 8).

The ventral walls of the genal sacs ("unterer Blätter der lamina maxillaris" of Becker, 1929) from the two sides of the head do not join medially, and do not project as far anteriorly as does the suspensory plate. They extend medially to the base of the salivary pump, but do not fuse with it. Instead, their medial margins run from the base of the salivary pump anteriorly as far as the tip of the food pump, to which they are lateral and somewhat ventral (Fig. 11). The efferent duct from the salivary pump lies between their two parallel medial margins.

The anterior margin of each ventral wall extends laterally to the anterior edge of the maxillary plate; along this margin it is continuous with the dorsal wall of the genal sac. The latter arises from an invagination along the anterior part of the dorsal suture, and extends posteriorly as far as the articulation of the mandibular lever. The dorsal layer of this invagination, along the ventral edge of the clypeus, gives rise to the epipharyngeal plate, which has already been discussed; the ventral layer of the invagination, along the dorsal edge of the maxillary plate, forms the dorsal wall of the genal sac (Fig. 13E). Thus both the dorsal and ventral walls of the genal sac are internal inflections of the anterior margins of the maxillary plate (Fig. 8); Becker (1929) termed these internal extensions the "laminae maxillares." The genal sacs are open only posteriorly; laterally they are closed by the maxillary plate, and medially by the medial wall of the genal sac, to be discussed next.

The medial wall of the genal sac is a rather complicated structure which is as difficult to describe and diagram as to dissect. It can best be understood by a study of transverse sections through the head (Fig. 13; indicated by broken lines). It is a delicate, thin-walled, double membrane attached to the hypopharyngeal wing and associated with the stylets and the levers of the stylets. In the posterior part of the head, it runs dorsally from the hypopharyngeal wing to the dorsal surface of the maxillary stylet (Fig. 13A). The maxillary lever lies between the two membranes near their posterior ends. More anteriorly,

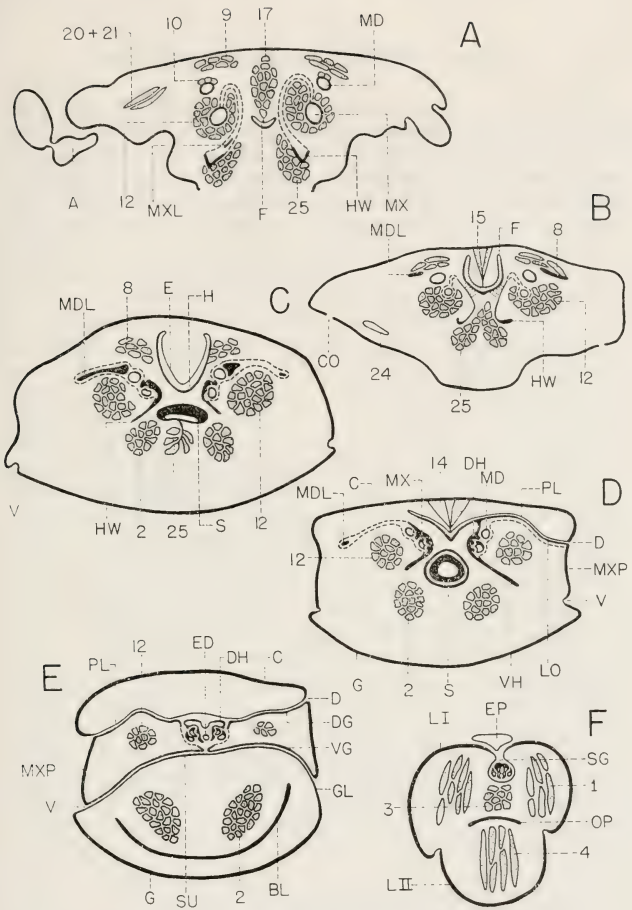


Figure 13. Transverse sections through the head of a fifth instar nymph. The medial walls of the genal sacs are indicated by broken lines, and the muscles are stippled. The right side of each section is slightly anterior to the left. Only the sclerotized structures and the muscles are shown. A, section at the level of the occipital foramen and the bases of the antennae. 30 X. B, section at the level of the striated plates; the fine fibrillae between the food pump and the hypopharyngeal wings are indicated by dotted lines. 30 X. C, section at the level at which the mandibular lever articulates with the mandibular stylet. 40 X. D, section at the level at which the lorum of the right side contacts the cranial exoskeleton. 40 X. E, section through the anterior part of the genal sacs, anterior to the salivary pump. 50 X. F, oblique section through the first two labial segments, showing the stylet bundle in the stylet groove. 50 X.

the medial wall comes to surround the base of the maxillary stylet, as shown in Figure 13B. At the point where the mandibular lever articulates with the mandibular stylet, the double membrane passes dorsolaterally to surround both the mandibular stylet and lever (Fig. 13C). At this point the medial wall of the genal sac resembles a sort of sling enclosing the stylets, the lever, and the dorsal surface of the hypopharyngeal wing. It probably helps to hold the stylets in position and to guide them onto the track-like ridges and grooves of the hypopharynx.

At the level of the lora (Fig. 13D, right side), the medial wall of the genal sac appears to consist of only one layer. Either the more dorsal membrane has ended at this point, or else the two membranes have fused together. The lateral part of the remaining one becomes fused here with the ventral surface of the lorum. Its medial part lies lateral to the stylets, holding them against the ridges of the dorsal surface of the hypopharyngeal wing (here merged with the lorum), and separating the stylets from the cavity of the genal sac. In Figure 13E, a section through the anterior part of the genal sacs, the membrane forms a short medial connection between the dorsal and the ventral walls of the sacs. It disappears at the anterior margin of the sacs, where the dorsal and ventral walls join. The general appearance of the medial wall of the genal sac is shown in Figures 4, 5, and 12. For simplicity it is omitted in most of the figures.

The two-layered medial wall of the genal sacs has been termed the "Wangensack" (Becker, 1929), the "membranous sling" (Hamilton, 1931), the "bristle pouch" (Snodgrass, 1935), the "visceraler Ast des Tentoriums" (Barth, 1952), and the "Stechborstenfalte" (Benwitz, 1956). Butt (1943) termed it the "maxillary sac" where it surrounds the maxilla, and the "mandibular sac" where it encircles the mandible; the two sacs together he termed the "bristle sac."

Mandibular Lever and Stylet

The mandibular lever (Figs. 4, 5, 12, 14), upon which the mandibular protractor muscles insert, is triangular in shape. One corner of the triangle is attached to the cranium at the dorsal suture, a little posterior to the point where the lorum contacts the cranium. A second corner articulates medially with

the thickened base of the mandibular stylet, while the third is unattached, projecting posteriorly in the head. The lateral and medial margins of the lever are heavily sclerotized, while the central part is membranous, continuing anteriorly directly into the dorsal wall of the genal sac without a break. The lateral margin of the lever is slightly longer than the medial margin,

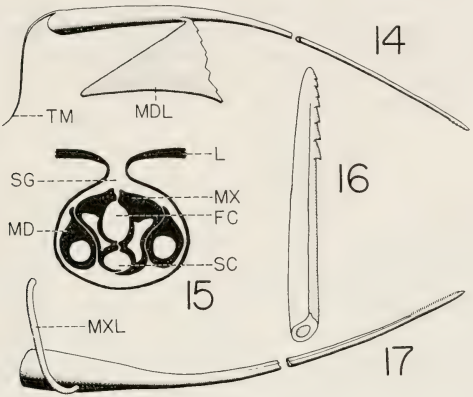


Figure 14. Dorsal view of the right mandibular stylet (middle part omitted) and lever.

Figure 15. Transverse section through the stylet bundle in the stylet groove of the labium (taken from the section shown in Figure 13F).

Figure 16. Detail of the tip of the right mandibular stylet, showing the teeth.

Figure 17. Dorsomedial view of the right maxillary stylet (middle part omitted) and lever.

the shape of the lever being somewhat different from that figured by Spooner (1938) for *Gelastocoris* sp.

Figure 14 shows the general form of the long, slender mandibular stylet. It is a hollow structure, approximately 2.5 mm. in length. From the medial side of the thickened base a very slender, sclerotized tendon extends posteriorly, providing an

insertion for one of the two groups of retractor muscles. A cross-section through the apical half of the mandibular stylet (Fig. 15) reveals that it is much wider ventrally than dorsally, allowing it to conform to the contours of the maxillary stylet within the stylet bundle. Along the lateral side of its tip are from five to seven tooth-like projections (Fig. 16), which extend posteriorly. Similar mandibular teeth have been reported in a great many Heteroptera, and appear to be of common occurrence. Since the mandibular stylets lie on the outside of the stylet bundle, these teeth are able to rasp against the tissue of the prey when the gelastocorid is feeding, and also help to anchor the tip of the stylet bundle during ingestion.

Maxillary Lever and Stylet

The maxillary lever (the "maxillary guide-rod" of Ekblom, 1929) is a slender, curved bar attached to the dorsal side of the base of the maxillary stylet (Figs, 4, 5, 12, 17). It curves ventrally and passes medial to the stylet to articulate with the lateral surface of the hypopharyngeal wing. As has been previously mentioned, the maxillary lever lies between the two membranous layers of the medial wall of the genal sac (Fig. 13A). Unlike the mandibular lever, it does not serve as a place for muscle attachments, and therefore the term lever is used here with some reservations. Neither Becker (1929; *Naucoris*) nor Ekblom (1929; several genera of Heteroptera) noted any muscular attachments on the maxillary lever.

The hollow maxillary stylet is shaped much like the mandibular one, although its base is somewhat thicker, since it provides a surface for the attachment of the protractor muscles as well as the retractors (Fig. 17). It is slightly longer than the mandibular stylet, being approximately 2.75 mm. in length, and lies ventral and medial to the latter within the cranium. Running along the medial surface of the stylet are two longitudinal grooves, separated by a ridge. Within the stylet bundle (Fig. 15), the two maxillary stylets lie together in the middle, and the opposed grooves form a dorsal *food canal* (*FC*) and a ventral *salivary canal* (*SC*); the ridge separating these lies ventral to the center, so that the salivary canal is narrower than the food canal. The stylet is broadest along its dorsal edge.

Along the medial surfaces of the tips of each stylet are longitudinal rows of anteriorly-directed bristles. Examination of the maxillae of two individuals revealed that the tip of the right maxilla differs from that of the left. The right maxilla bears four bristle rows, as shown in Figure 18B; the two outer ones, located on the dorsal and ventral margins, consist of rather fine hairs projecting outwards, while the two inner ones are composed of stiffer bristles which extend medially. The latter are located along the ridge dividing the food and salivary canals and along the dorsal margin of the dorsal groove. The left

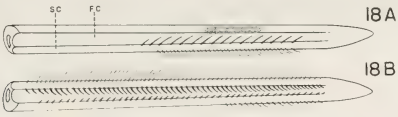


Figure 18. Details of the medial surfaces of the tips of the maxillary stylets, showing the rows of bristles. A, left maxillary stylet. B, right maxillary stylet.

maxilla bears a tuft of fine hairs on the dorsal margin of the dorsal groove, along with only two rows of bristles, one on the ventral margin and one on the separating ridge (Fig. 18A). These rows are shorter than those of the right maxilla. The bristles of the more dorsal row are stiffened and project medially. Longitudinal sections through the stylet bundle reveal that the bristles of the opposed separating ridges on the two stylets interlock, thus holding the right and left maxillae together. It is possible that the maxillary hairs and bristles help to sift out particulate matter from the ingested food. Many authors have reported similar rows of maxillary bristles in other Heteroptera, and some asymmetry in their arrangement seems to be common.

Labium and Labrum

The main body of the gelastocorid beak is formed by the labium, the labrum being only a dorsal flap overlapping its base. The labrum (Figs. 3, 5, 9) is shaped like a broad triangle, with a wide posterior base and curved sides ending in an anteriorly

projecting apex. Its base is attached by a membrane to the anterior border of the clypeus, as far as the margins of the maxillary plates. Fused to its ventral surface is the anterior portion of the epipharyngeal plate, and the epipharyngeal projection extends a short distance anterior to it (Fig. 9).

The labium is attached to the cranium by a membrane extending from the ventral part of its posterior border to the anterior edge of the gula. This membrane ends at the anterior margins of the maxillary plate. Dorsally, the labium does not articulate with the exoskeleton; here the most basal part of the first (or basal) labial segment is membranous, and is partially or wholly fused with the anterior edge of the suspensory plate. The labium is composed of four segments, of which the second and fourth

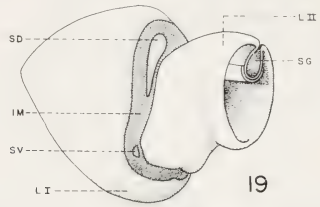


Figure 19. Anterolateral view of the first two segments of the labium, showing the dorsal and ventral intersegmental sclerites.

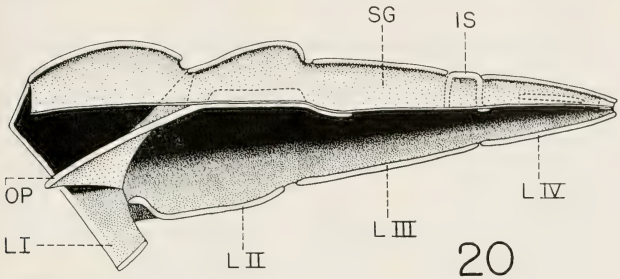
are the shortest and the third the longest. Each is cylindrical, its dorsal part being membranous and invaginated to form the stylet groove which contains the apical portions of the four stylets (Figs. 19, 20, 21).

The most basal labial segment is much longer dorsally than ventrally (Figs. 19, 20). Its ventral part is often concealed by the anterior edge of the gula. The posterior margin of the dorsal side is not straight, but is somewhat V-shaped, the apex of the V projecting anteriorly and the two arms extending posteriorly. The basal portion of the dorsal side is membranous, while the anterior portion is heavily sclerotized; the labrum overlaps the membranous part.

In the connecting membrane between the first and second segments are two pairs of intersegmental sclerites (Fig. 19), an

elongate, dorsally located one, and a much smaller, ventral one, which is roughly oval in shape. These provide insertions for parts of the main levator and depressor muscles of the labium.

The second labial segment is the most complex and irregularly shaped of the four. The midventral part of its basal margin is bent inwards, forming a short projection, and a second, larger



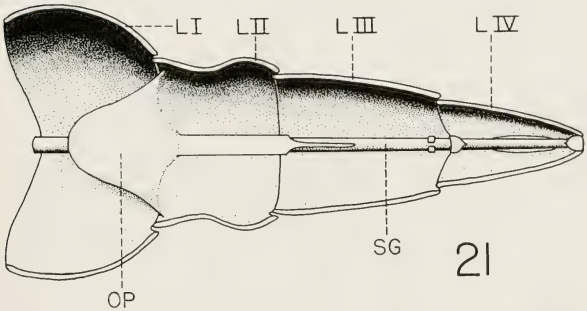


Figure 20. Lateral view of the inner surface of the left half of the labium. The labium has been cut down the midline, and the right half has been removed. The broken lines indicate the pigmented, sclerotized structures supporting the stylet groove.

Figure 21. View of the inner surface of the dorsal half of the labium. The ventral half has been removed. The unstippled areas anterior to the oblique plate represent the pigmented, sclerotized structures supporting the stylet groove.

apodeme originates from its basal margin dorsally (Figs. 20, 21) The latter is a posterior continuation of the entire dorsal half of that margin, extending into the cavity of the first labial segment in the form of a broad, flat *oblique plate* (*OP*). It serves as a point of attachment for two labial muscles. Apodemes identical to the oblique plate in both form and position have been described by Becker (1929) in *Naucoris*, and by Butt (1943) in *Notonecta*. The author has also observed them in *Nepa*, *Ranatra*, *Pelocoris*, and *Lethocerus*. Griffith (1945) reported a structure in corixids which he considered to be homologous with this apodeme, although Benwitz (1956) disagreed with his interpretation. In *Gelastocoris*, the floor of the stylet groove appears to be reinforced, in the second labial segment, by an underlying sclerotized shelf which is continuous with the base of the oblique plate (Fig. 21). This shelf, which is heavily pigmented, extends into the posterior part of the stylet groove of the third labial segment. Similar supporting structures of the stylet groove have been described in *Naucoris* by Becker (1929).

The third and fourth segments are relatively simple and cylindrical. The stylet groove is located more centrally in these than in the two preceding segments. Between the two terminal segments are a pair of sclerites which resemble short rods on the dorsal outer surface (Fig. 20, *IS*). They lie side by side directly above the stylet groove, and the dorsal margins of the third and fourth segments are somewhat notched to accommodate them. The anterior and posterior ends of each sclerite extend ventrally to encircle the stylet groove beneath them (Figs. 20, 21). Of the two rings thus formed, the posterior one is incomplete ventrally while the anterior one is complete. These structures apparently support the stylet groove. Similar sclerites have been observed between the two terminal sclerites of *Benacus*, *Gerris*, and *Velia* ("palpus labialis" of Leon, 1897), *Belostoma* ("labiappendices" of Crampton, 1921), *Naucoris* ("Läppchen" of Becker, 1929), and *Nepa* ("labial appendages" of Hamilton, 1931). The author has also observed them in *Notonecta*. The stylet groove of the terminal segment is further supported by a pair of pigmented, sclerotized bars lying in the walls of the sides of the groove, and by a third sclerotized ring which encircles the groove at the tip of the segment (Fig. 21). Similar supporting structures have

been reported in the terminal labial segments of *Sphaerodema* and *Anisops* (Qadri, 1951) and of *Leptocorisa* (Akbar, 1957).

Muscles of the Head

In the following section, an attempt has been made to list, for each muscle, similar muscles which have been reported in other Heteroptera. Those which are listed are included because both their origins and their insertions, as described in the literature, are the same or very similar to those of the corresponding muscle in *Gelastocoris*. Whether or not they are actually homologous to the gelastocorid muscle which they resemble cannot, in most cases, be definitely stated.

In Figures 22 through 28, the muscles are designated by the numbers given below.

Labial muscles

1. M. LEVATOR LABII (Figs. 13F, 22, 23, 24, 25)

A very well developed, paired muscle.

Origin: Ventral surface of the suspensory plate, anterior to the genal sacs.

Insertion: Posterior margin of the second labial segment, both dorsally (on either side of the stylet groove) and laterally, as far as the ventral intersegmental sclerites. Some strands also insert onto the dorsal and ventral intersegmental sclerites.

Action: Raises the labium; probably also allows some lateral movement.

Similar muscles: Second adductors of the labium (*Notonecta;* Butt, 1943); abductor of the labium (*Leptocorisa;* Akbar, 1957).

2. M. DEPRESSOR LABII PRIMUS (Figs. 13C-E, 22, 24, 25)

A well developed, paired muscle.

Origin: Medial surface of the hypopharyngeal wing, just posterior to the salivary pump.

Insertion: Posterior margin of the second labial segment, on either side of the ventromedial apodeme; extends along the ventral side as far as the ventral intersegmental sclerites. A few strands appear to insert on the latter.

Action: Lowers the labium.

Similar muscles: First adductors of the labium (*Notonecta* and *Oncopeltus;* Butt, 1943); extrinsic adductor of the labium (*Leptocorisa;* Akbar, 1957).

3. M. TRANSVERSALIS LABII PRIMUS (Figs. 13F, 22, 24)

A short, thick, unpaired muscle.
Origin: Dorsal surface of the oblique plate of the labium.
Insertion: Floor of the stylet groove of the first labial segment.
Action: Depresses the floor of the stylet groove, possibly forcing together the dorsal lips of the groove. Possibly lowers the labium by raising the oblique plate (?).
Similar muscles: Median transverse muscles of the bristle trough (*Notonecta;* Butt, 1943).

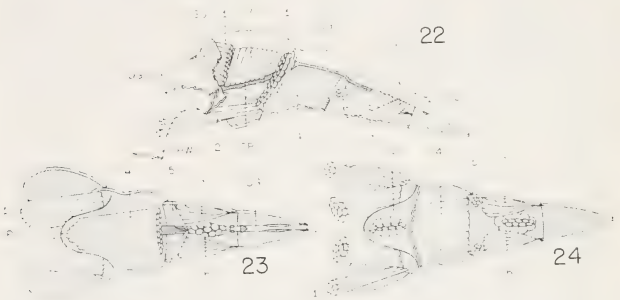


Figure 22. Lateral view of the labium, with the exoskeleton removed on the right side in order to show the muscles. The oblique plate and the supporting structures of the stylet groove are heavily stippled. Part of muscle no. 1 has been removed in order to show muscle no. 3. Muscles nos. 1 and 5 are omitted on the left side; muscle no. 7 and part of muscle no. 4 are omitted on the right side.

Figure 23. View of the inner surface of the dorsal half of the labium, showing the muscles. The supporting structures of the stylet groove are heavily stippled.

Figure 24. View of the inner surface of the ventral half of the labium, showing the muscles.

4. M. DEPRESSOR LABII SECUNDUS (Figs. 13F, 22, 23, 24).

A well developed, unpaired muscle.
Origin: Ventral surface of the oblique plate of the labium.
Insertion: Posteroventral margin of the third labial segment.
Action: Lowers the third and fourth labial segments.

Similar muscles: M. depressor labii (*Naucoris;* Becker, 1929); third adductors of the labium (*Notonecta;* Butt, 1943); muscle group B (?) (*Rhamphocorixa;* Griffith, 1945).

5. M. TRANSVERSALIS LABII SECUNDUS (Figs. 22, 23, 24).

A slender, paired muscle.

Origin: Posterolateral margin of the third labial segment.

Insertion: Lateral margin of the anterior portion of the sclerotized pigmented shelf supporting the stylet groove in the third labial segment.

Action: Moves the third and fourth labial segments laterally (?).

Similar muscles: Muskel der Endoskelettplatte (?) (*Naucoris;* Becker, 1929); M. transversalis 1 (*Cimex;* Kemper, 1932); first transverse muscles of the bristle trough (?) (*Notonecta* and *Oncopeltus;* Butt, 1943).

6. M. TRANSVERSALIS LABII TERTIUS (Figs. 22, 23, 24)

A fairly well developed, unpaired muscle.

Origin: Ventral wall of the third labial segment.

Insertion: Floor of the stylet groove in the anterior part of the third labial segment, anteriorly to the posterior sclerotized ring.

Action: Depresses the floor of the stylet groove, possibly forcing together the dorsal lips of the groove.

Similar muscles: Muskel der Endoskelettbildung (?) (*Naucoris;* Becker, 1929); M. transversalis 2 (*Cimex;* Kemper, 1932); second transverse muscles of the bristle trough (*Notonecta;* possibly also *Oncopeltus;* Butt, 1943); first transverse muscles of the labial plate (*Leptocorisa;* Akbar, 1957).

7. M. RETRACTOR SEGMENTI ULTIMI LABII (Figs. 22, 23, 24)

A well developed, fan-shaped, paired muscle.

Origin: Posterolateral walls of the third labial segment, reaching nearly to the stylet groove dorsally and nearly to the midline ventrally.

Insertion: On a slender sclerotized strand from the posterolateral margin of the fourth labial segment.

Action: Pulls the fourth labial segment posteriorly (simultaneous contraction of the muscles of both sides) or laterally (contraction of only one muscle).

Similar muscles: Levatormuskel des vierten Unterlippengliedes (*Naucoris;* Becker, 1929); Adduktor 6 (*Cimex;* Kemper, 1932); retractors of the terminal segment (*Notonecta* and *Oncopeltus;* Butt, 1943).

Muscles of the stylets

8. M. PROTRACTOR SETAE MANDIBULARIS PRIMUS (Figs. 13B, C, 25, 26)

A paired muscle, running dorsal to the mandibular lever and to the mandibular and maxillary stylets.

Origin: Ventromedial surface of the lorum, and the side of the food pump.

Insertion: Lateral margin of the mandibular lever, just anterior to M. protractor setae mandibularis secundus.

Action: Moves the mandibular lever medially, thus extending the mandibular stylet.

Similar muscles: Protractor der Mandibularborste (*Naucoris;* Becker, 1929); hypopharyngeal-mandibular muscle (*Notonecta* and *Oncopeltus;* Butt, 1943); protractor of mandible (*Rhamphocorixa;* Griffith, 1945); M. protractor mandibulae (*Triatoma;* Barth, 1952); M. protractor setae mandibularis (*Corixa;* Benwitz, 1956); protractor of mandibular stylets (*Leptocorisa;* Akbar, 1957).

9. M. PROTRACTOR SETAE MANDIBULARIS SECUNDUS (Figs. 13A, 25, 26)

A paired muscle, running dorsal to the mandibular lever, the mandibular and maxillary stylets, and the food pump.

Origin: Inner surface of the clypeus, just lateral to the midline, and between the U-shaped ridge and the point where the clypeal connectives of the food pump contact the cranium.

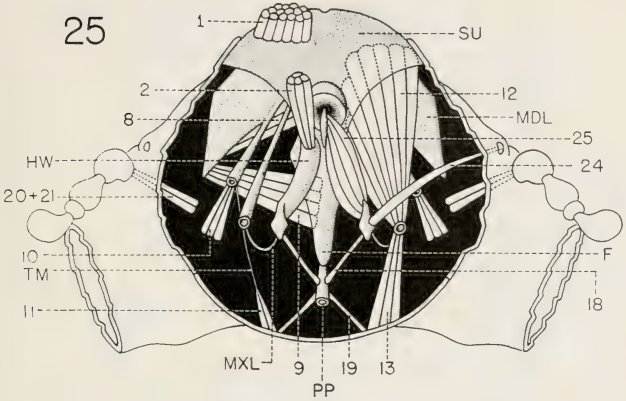
Insertion: Lateral margin of the mandibular lever, between the insertion of M. protractor setae mandibularis primus and the apex of the lever.

Action: Same as M. protractor setae mandibularis primus.

Similar muscle: Protractor muscles of the mandible (?) (*Velia;* Ekblom, 1926).

10. M. RETRACTOR SETAE MANDIBULARIS PRIMUS (Figs. 13A, 25, 26)

A paired muscle, better developed than M. retractor setae mandibularis secundus.



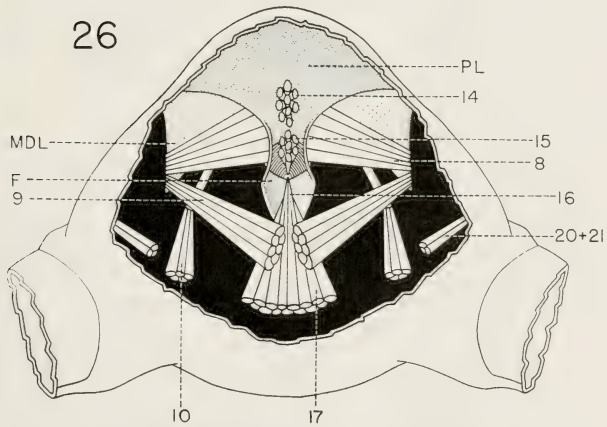


Figure 25. Ventral view of the head, with most of the gula removed in order to show the muscles. The compound eyes have been cut off at their bases. Muscles nos. 12, 13, 24, and 25 are omitted on the right side, and muscles nos. 1, 2, 8, and 9 are omitted on the left. Muscles nos. 16 and 17 are not shown.

Figure 26. Dorsal view of the head, with much of the clypeus and vertex removed to show the more dorsal muscles. The compound eyes have been cut off at their bases. The more ventral muscles are omitted, and the maxillary stylets and hypopharyngeal wings are not shown.

Origin: Roof of the cranium, on the more posterior of the two short grooves lying lateral to the ocellus (see Fig. 1).

Insertion: Dorsal side of the base of the mandibular stylet.

Action: Retracts the mandibular stylet.

Similar muscles: Retractor Nr. 1 der Mandibularborste (*Naucoris;* Becker, 1929); retractor "rm_1" of mandible (*Aphanus* and *Myrmus;* Ekblom, 1926 and 1930).

11. M. RETRACTOR SETAE MANDIBULARIS SECUNDUS (Fig. 25)

A short, slender, weakly developed, paired muscle.

Origin: Dorsal margin of the occipital foramen, just dorsal to the origin of M. retractor setae maxillaris.

Insertion: End of a long, slender, sclerotized tendon extending from the medial side of the base of the mandibular stylet.

Action: Retracts the mandibular stylet.

Similar muscles: Retractor muscle "rm" of the mandibular seta (*Salda; Nabis, Corixa, Aphanus, Myrmus,* and *Hydrometra;* Ekblom, 1926 and 1930); Retractor Nr. 2 der Mandibularborste (*Naucoris;* Becker, 1929); retractor of mandible (*Notonecta;* Butt, 1943; and *Rhamphocorixa;* Griffith, 1945); M. retractor mandibulae (*Triatoma;* Barth, 1952); M. retractor setae mandibularis (*Corixa;* Benwitz, 1956); retractor "a" of mandibular stylets (*Leptocorisa;* Akbar, 1957).

12. M. PROTRACTOR SETAE MAXILLARIS (Figs. 13A-E, 25)

An extremely well developed, paired muscle, surrounding the basal part of the maxillary stylet, and lying ventral to the mandibular lever and stylet.

Origin: Along the lateral surface of the hypopharyngeal wing in the region of the salivary pump, and along the inner surface of the anterior part of the genal sac.

Insertion: Encircling the base of the maxillary stylet.

Action: Extends the maxillary stylet.

Similar muscles: Maxillary protractors (*Salda, Nabis, Aphanus,* and *Hydrometra;* Ekblom, 1926); Protractor der Maxillenborste (*Naucoris;* Becker, 1929); protractor of maxilla (*Notonecta* and *Oncopeltus;* Butt, 1943); Mm. protractores maxillae primus et secundus (*Triatoma;* Barth, 1952); Mm. protractores setae maxillaris (*Corixa;* Benwitz, 1956); protractors "b" and "c" of maxillary stylets (*Leptocorisa;* Akbar, 1957).

13. M. RETRACTOR SETAE MAXILLARIS (Fig. 25)

A paired muscle.

Origin: Dorsal margin of the occipital foramen, just ventral to the origin of M. retractor setae mandibularis secundus.

Insertion: Dorsal side of the base of the maxillary stylet, posterior to M. protractor setae maxillaris.

Action: Retracts the maxillary stylet.

Similar muscles: Maxillary retractors (*Salda, Nabis, Aphanus, Hydrometra,* and *Corixa;* Ekblom, 1926 and 1930); Retractor der Maxillenborste (*Naucoris;* Becker, 1929); retractor of maxilla (*Notonecta* and *Oncopeltus;* Butt, 1943; and *Rhamphocorixa;* Griffith, 1945); Mm. retractores maxillae primus et secundus (*Triatoma;* Barth, 1952); M. retractor setae maxillaris (*Corixa;* Benwitz, 1956); retractor of maxillary stylets (*Leptocorisa;* Akbar, 1957).

Muscles of the food pump

All but the few posteriormost strands of the muscles of the food pump are cibarial in origin, lying anterior to the frontal ganglion. The literature indicates that the cibarial muscles may comprise a single group, as in *Ranatra* and *Belostoma* (Marks, 1958) or may be subdivided, as in *Corixa* (Benwitz, 1956) or *Leptocorisa* (Akbar, 1957). It appears that the grouping of the muscles of the food pump is a variable feature, the different groups shifting as new needs arise. Therefore no extensive attempt will be made to list similar muscles from the literature for each of the four groups seen in *Gelastocoris.* The only other heteropteran which will be considered here is *Pelocoris femoratus;* since the position of the frontal ganglion is the same in this species as in *Gelastocoris oculatus* (see Discussion), the muscle groups of the two insects are directly comparable, and are almost certainly homologous.

14. M. DILATOR CIBARII PRIMUS (Figs. 13D, 26, 27)

Fans out dorsal to the point of insertion, so that it appears V-shaped in transverse sections.

Origin: Inner surface of the clypeus.

Insertion: On the epipharyngeal tendons of Group 1, anterior to the striated plates.

Action: Elevates the anterior part of the epipharynx, thus dilating the food pump.

Similar muscle: Anterior part of Muscle Group 1 (*Pelocoris:* Marks, 1959).

15. M. DILATOR CIBARII SECUNDUS (Figs. 13B, 26, 27)

Similar, in appearance, to M. dilator cibarii primus.

Origin: Inner surface of the clypeus, just posterior to M. dilator cibarii primus.

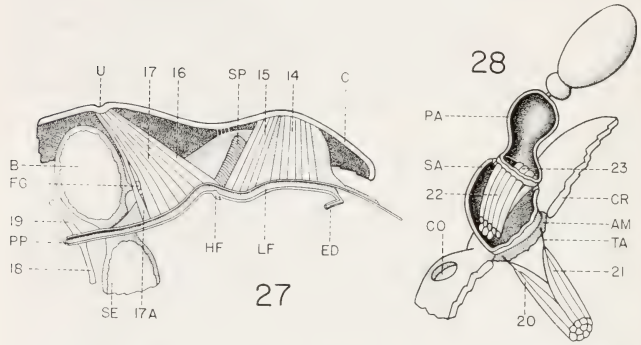


Figure 27. Lateral view of the cibarial and pharyngeal muscles. The head has been cut down the midline, and the left halves of the food pump, brain, and subesophageal ganglion are shown. The lateral part of the clypeus has been cut off, and the salivary pump is omitted.

Figure 28. Medial view of the left antenna, with the medial walls of the scape and the pedicel removed to show the muscles. The cranial exoskeleton has been cut away from the medial side of the base of the antenna to reveal the articular membrane.

Insertion: On the epipharyngeal tendons of Group 2, between the striated plates.

Action: Elevates the epipharynx in the region of the striated plates, thus dilating the food pump; raises and lowers the striated plates.

Similar muscle: Posterior part of Muscle Group 1 (*Pelocoris;* Marks, 1959).

16. M. DILATOR CIBARII TERTIUS (Figs. 26, 27)

This unpaired muscle is contiguous with M. dilator cibarii quartius, differing from it only in its insertion. The two muscle groups are difficult to separate in dissections. They form an extensive, fan-shaped bundle, which runs posterodorsally from its points of insertion, passing ventral to M. protractor setae mandibularis secundus.

Origin: U-shaped medial ridge of the clypeus, between the ocelli.

Insertion: On the epipharyngeal tendons of Group 3, on the united posteromedial corners of the striated plates.

Action: Moves the striated plates back and forth in an anterior-posterior direction.

Similar muscle: Muscle Group 2 (*Pelocoris;* Marks, 1959).

17. M. DILATOR CIBARII QUARTIUS (Figs. 13A, 26, 27)

See comments under the preceding muscle. The frontal ganglion lies within this muscle group, just anterior to the few most posterior strands. Strictly speaking, therefore, these last few strands (Fig. 27, *17 A*) should be termed *M. dilator praepharyngis,* and the point of their insertion represents the anterior pharynx. The cibarial and pharyngeal elements appear, however, to be merged into one muscle group.

Origin: In common with M. dilator cibarii tertius.

Insertion: On the epipharyngeal tendons of Group 4, posterior to the striated plates.

Action: Elevates the posterior part of the epipharynx, thus dilating the food pump.

Similar muscle: Muscle Group 3 (*Pelocoris;* Marks, 1959).

Muscles of the posterior pharynx

18. M. DILATOR POSTPHARYNGIS VENTRALIS (Figs. 25, 27)

A very slender, paired muscle.

Origin: Tip of the hypopharyngeal wing.

Insertion: Ventrolateral surface of the posterior pharynx, just posterior to where the pharynx emerges from between the brain and the subesophageal ganglion.

Action: Acting along with M. dilator postpharyngis dorsalis, dilates the posterior pharynx.

Similar muscles: Mm. dilatatores oesophagi "mr_2" (*Naucoris;* Becker, 1929); Mm. dilatatores postpharyngis ventrales (*Corixa;* Benwitz, 1956).

19. M. DILATOR POSTPHARYNGIS DORSALIS (Figs. 25, 27)

A very slender, paired muscle.

Origin: Dorsal margin of the occipital foramen, just medial to Mm. retractores setarum mandibularis secundus and maxillaris.

Insertion: Dorsolateral surface of the posterior pharynx, dorsal to M. dilator postpharyngis ventralis.

Action: Acting along with M. dilator postpharyngis ventralis, dilates the posterior pharynx.

Similar muscles: Mm. dilatatores oesophagi "mr_1" (*Naucoris;* Becker, 1929); dilator of postpharyngeal region (*Rhamphocorixa;* Griffith, 1945); Mm. dilatatores postpharyngis dorsales (*Corixa;* Benwitz, 1956).

Muscles of the antenna

20. M. LEVATOR SCAPI (Figs. 13A, 25, 26, 28)

A slender muscle, on either side of the head, joined with M. depressor scapi for most of its length. These two muscles separate just before their insertions.

Origin: Roof of the cranium, on the more anterior of the two short grooves lying lateral to the ocellus (see Fig. 1).

Insertion: Slender sclerotized tendon in the anterior part of the articular membrane joining the first antennal segment (scape) to the cranium.

Action: Raises the entire antenna (pulls it anteriorly).

Similar muscles: Part of "Muskelzüge des Kopfes inseriert an der Gelenkhaut I" (*Nepa* and *Ranatra;* Hüfner, 1939); M. levator ? scapi (*Corixa;* Benwitz, 1956).

21. M. DEPRESSOR SCAPI (Figs. 13A, 25, 26, 28)

See comments for the preceding muscle.

Origin: In common with M. levator scapi.

Insertion: Slender sclerotized tendon in the posterior part of the articular membrane joining the scape to the cranium.

Action: Lowers the entire antenna (pulls it posteriorly).

Similar muscles: Part of "Muskelzüge des Kopfes inseriert an der Gelenkhaut I" (*Nepa* and *Ranatra;* Hüfner, 1939); M. depressor scapi (*Corixa;* Benwitz, 1956).

22. M. SCAPO-PEDICELLARIS MEDIALIS (Fig. 28)

A short, broad muscle.

Origin: Anterior wall of the scape, just medial to M. scapo-pedicellaris lateralis.

Insertion: Ventromedial margin of the base of the second antennal segment (pedicel).

Action: Moves the last three antennal segments ventromedially.

Similar muscles: Part of "Scapus-muskulatur" (*Notonecta, Naucoris,* and *Aphelocheirus;* Hüfner, 1939).

23. M. SCAPO-PEDICELLARIS LATERALIS (Fig. 28)

A short, broad muscle.

Origin: Anterior wall of the scape, just lateral to M. scapo-pedicellaris medialis.

Insertion: Dorsolateral margin of the base of the pedicel.

Action: Moves the last three antennal segments dorsolaterally.

Similar muscles: Part of "Scapus-muskulatur" (*Notonecta, Naucoris,* and *Aphelocheirus;* Hüfner, 1939).

Muscle of the cephalic gland

24. M. DILATOR ORIS GLANDULAE CAPITIS (Figs. 13B, 25)

A long, slender muscle, lying ventral to all other structures in the lateral part of the head.

Origin: Tip of the hypopharyngeal wing.

Insertion: Sclerotized flap on the medial wall of the mouth of the cephalic gland.

Action: Pulls the mouth of the cephalic gland medially, to lie beneath the orifice in the exoskeleton, thus allowing secretion to escape to the exterior (see Parsons, in press, where this muscle is termed "muscle inserting on sclerotized flap").

Similar muscles: Das Reservoir öffnender Muskel (*Naucoris;* Becker, 1929).

Muscle of the salivary pump

25. M. RETRACTOR PISTILLI (Figs. 13A-C, 25)

A well-developed, paired muscle.

Origin: Posterior portion of the hypopharyngeal wing, ventromedially and ventrolaterally.

Insertion: Side of the plate-like tendon of the salivary pump.

Action: Retracts the invaginated posterior wall of the pump, thus dilating it.

Similar muscles: Muskel der Speichelpumpe (*Naucoris;* Becker, 1929); aspirator muscles (*Nepa;* Hamilton, 1931); dilator muscles of the syringe (*Notonecta;* Butt, 1943); M. retractor pistilli (*Triatoma;* Barth, 1952; and *Corixa;* Benwitz, 1956); muscles of salivary syringe (part only) (*Leptocorisa;* Akbar, 1957).

DISCUSSION

The three littoral families Gelastocoridae, Ochteridae, and Saldidae share several external structural similarities which suggest that they are closely related to each other. China (1933) has expressed the belief that all the littoral families had a common origin. The evidence presented in the literature seems to indicate that the gelastocorids arose from ochterid-like ancestors (Reuter, 1910; China, 1933, 1955b), and that the shore-dwelling Heteroptera are rather generalized members of that order. Several primitive features of their anatomy support the latter view. Two cephalic characteristics, the possession of ocelli and four-segmented antennae, are regarded by Reuter (1910) and China (1955b) as primitive. Some authors have considered the Saldidae (Osborn, 1895; Ekblom, 1929) or the Ochteridae (Reuter, 1910) to be the most primitive living families of the Heteroptera.

Most authorities agree that the littoral bugs represent a stage in the evolution of the aquatic or semi-aquatic forms, their habitat being a transition between the terrestrial and aquatic environments (in the following discussion, the terms "aquatic" and "Hydrocorisae" will be used for those families which live beneath the surface of the water, while "semi-aquatic" or "Amphibicorisae" will refer to those which inhabit the surface film). However, differences of opinion have arisen as to which of the littoral families are related to the semi-aquatic forms, and which to the aquatic ones.

The division of the Heteroptera into two groups, based upon the condition of the antennae, has been used by many workers such as Handlirsch (1908). The terrestrial and semi-aquatic families, along with the Saldidae, are included in the Gymnocerata because of their long, free antennae, while the totally aquatic families plus the gelastocorids and ochterids are termed Cryptocerata. In the latter group, the antennae are relatively short and, except in *Aphelocheirus* and in the Ochteridae, are concealed beneath the eyes. This system of classification was criticized by Reuter (1910), who, feeling that the gymnocerate-cryptocerate split was not a natural division, set up six heteropteran series. In the Series Hydrobiotica he grouped all the littoral, aquatic, and semi-aquatic families, placing the rest of

the Gymnocerata in five other series. His system was based primarily upon the character of the wings, the eggs, and the sternal sclerites, features which, according to Spooner (1938), have been shown to be rather undependable for phylogenetic purposes.

The relationship between the littoral and the totally aquatic forms has not been generally agreed upon. De la Torre-Bueno (1923) considered the totally aquatic families to be derived from saldid-like ancestors, the Ochteridae representing an intermediate condition. Ekblom (1929) also believed the saldids to represent the ancestral aquatic bugs. China (1955b), however, proposed that the totally aquatic families arose from "Proto-Ochteridae," while the "Proto-Saldidae" gave rise to the semi-aquatic forms. His system corresponds, in this respect, to the old gymnocerate-cryptocerate division, although he used Dufour's (1833) terms Hydrocorisae (for the aquatic families plus the ochterids and gelastocorids), Geocorisae (for the terrestrial groups), and Amphibicorisae (for the semi-aquatic forms and the saldids).

Spooner (1938) considered the ochterids and gelastocorids to form a bridge between the aquatic and semi-aquatic bugs, and, unlike China, he believed them to be more closely related to the latter than to the former. His classification was based primarily upon the structure of the labrum and the mandibular lever. Using the terminology of Dufour (1833) he placed the Ochteridae, Gelastocoridae, and semi-aquatic families in the Amphibicorisae, the Saldidae and terrestrial families in the Geocorisae, and all the aquatic forms except the corixids in the Hydrocorisae. He considered the Corixidae different enough to constitute a fourth group, the Sandaliorrhyncha (a term proposed by Börner, 1904).

The problem of the phylogenetic position of the Saldidae and Ochteridae deserves further attention, and more morphological work upon these two families is needed. The present study has revealed a few features in the structure of the gelastocorid head which may shed some light on whether the Gelastocoridae are more similar to the aquatic or to the semi-aquatic Heteroptera. This purpose is somewhat hindered by the fact that only one of the two genera of Gelastocoridae is here represented. Another obstacle is that, in general, more morphological work has been

done upon the aquatic families than upon the semi-aquatic ones, and hence it is easier to make comparisons with the former than with the latter.

Several features in the head of *Gelastocoris* link this insect with the aquatic Heteroptera. Some of these are seen in its external anatomy. First, there is the absence of a distinct anteclypeus; of the genera examined by Spooner (1938), only four showed this condition; *Gelastocoris, Ochterus* (Ochteridae), and the aquatic bugs *Pelocoris* (Naucoridae) and *Notonecta* (Notonectidae). A second similarity between *Gelastocoris* and the latter two genera is the absence of external loral or paraclypeal sclerites in all three. Spooner claimed that these sclerites are smaller in *Pelocoris* and *Notonecta* than in any other forms which he examined; his mistaking, in *Gelastocoris,* of the maxillary plate for the external lorum has already been discussed. The present author has examined *Notonecta* and *Pelocoris* and concluded that their lora, like those of *Gelastocoris,* are contained entirely within the head. Butt (1943) reported the absence of external lora in *Notonecta,* and Rawat (1939) does not mention any loral sclerite in *Naucoris* (Naucoridae).

A third external resemblance to the aquatic forms lies in the shortness and stoutness of the labium. The beaks of the semi-aquatic bugs are, in general, longer and more slender. A fourth similarity is the presence of the two intersegmental sclerites between the last two segments of the labium. This character is not diagnostic, however, since these sclerites are not restricted to the aquatic Heteroptera; Leon (1897) has reported their presence in the semi-aquatic genera *Velia* and *Gerris.* The short, concealed antennae form a fifth point of resemblance between gelastocorids and the Hydrocorisae, but one which may be less significant than the first three preceding ones. Reuter (1910) suggested that the reduced length of the antennae of *Ochterus* may be an adaptation to the burrowing habit, and Todd (1955) has also proposed this with regard to the gelastocorids. This antennal reduction could have taken place in the ancestral Hydrocorisae (the littoral "Proto-Ochteridae" of China, 1955b) as an adaptation to burrowing; it could also be argued, however, that the reduction did not occur in the Hydrocorisae until after they entered the water, and that in the gelastocorids it has been

an independent development. Hüfner (1939) has described much variation in the general form of the antennae of the aquatic Heteroptera. It seems, therefore, that the length and form of the gelastocorid antenna is a somewhat unreliable phylogenetic character.

Five internal characteristics of the gelastocorid head may indicate a relationship with the aquatic Heteroptera. The food pump of *Gelastocoris* is in many ways similar to that of *Pelocoris*, and also shows some resemblances to that of *Notonecta*. Since this is a point worthy of some discussion, it will be considered in some detail later. Secondly, as was mentioned earlier, the oblique plate of the labium is also found in the aquatic families Notonectidae, Naucoridae, Belostomatidae, and Nepidae; to the author's knowledge, it has never been reported in any semi-aquatic or terrestrial forms. The striking similarity of the labial musculature of *Gelastocoris* to that of *Notonecta* forms a third point of comparison; the two bugs appear to be identical in this character except that *Notonecta* possesses muscles in the terminal segment (Butt, 1943) which are lacking in *Gelastocoris*. A fourth internal similarity is the presence, in *Gelastocoris*, of a maxillary lever. Ekblom (1929) found this structure in the Geocorisae and in some of the Hydrocorisae which he examined, but reported its absence in the Amphibicorisae. The fifth resemblance is the presence of cephalic glands in *Gelastocoris;* this has been discussed in another paper (Parsons, in press). Such glands are present in representatives of all the families of water bugs, but have never been reported in the semi-aquatic forms.

According to Spooner (1938), two features of the heads of gelastocorids and ochterids link them more closely to the semi-aquatic than to the aquatic forms. His first and most convincing piece of evidence is the presence of the epipharyngeal projection extending beyond the apex of the labrum. Spooner studied a wide variety of genera, and found this projection only in the semi-aquatic bugs and in *Ochterus* and *Gelastocoris*. The present study confirms its presence in the last. His evidence from the mandibular levers, however, is less convincing. Spooner cites the work of Ekblom (1929), who distinguished four types of mandibular levers. The first of these is typical of Geocorisae, the second of Hydrocorisae, the third of Sandaliorrhyncha, and the

fourth of Amphibicorisae. Type II is three-branched and attached directly to the stylet, while Type IV is quadrangular and attached to the stylet by a projection from one of its faces. Spooner considered the mandibular levers of *Ochterus* and *Gelastocoris* to be of this last type.

Spooner's argument on the grounds of the mandibular lever appears weak for two reasons. First, he found much variation, especially within Ekblom's Types I and II; in the latter he found three fairly distinct sub-types. China (1955a) has already questioned the phylogenetic significance of the mandibular levers in the Geocorisae. Secondly, Spooner admits that the levers of *Ochterus* and *Gelastocoris* differ somewhat from the others of Type IV. They are triangular in shape rather than quadrangular. In *Ochterus*, the projection joining the lever to the stylet is very short and is attached to the edge of the lever rather than to its face, while in *Gelastocoris* the projection appears to be absent, the lever articulating directly with the stylet. In the author's opinion, the mandibular levers of these two insects, as described by Spooner, bear more resemblance to the three-branched levers of the Hydrocorisae, and should not be placed in the same group as those of the Amphibicorisae. In *Gelastocoris*, as was earlier described, the two posterior edges of the lever are heavily sclerotized while the middle part is membranous, continuing anteriorly into the dorsal wall of the genal sac. A similar condition is found in the lever of *Pelocoris*. Spooner diagrammed only a slender, elbow-like bent rod for this genus; I have examined the *Pelocoris* lever, however, and found it to have a triangular, membranous, middle part which, like that of *Gelastocoris*, passes into the wall of the genal sac. Spooner states that the attachment of the levers to the stylets is direct in *Ochterus* and *Gelastocoris;* this is also characteristic of the levers of the Hydrocorisae, as described by him.

The cephalic characters of the gelastocorids appear, to the author, to be more like those of the aquatic than of the semi-aquatic Heteroptera. The epipharyngeal projection seems to be the best evidence in support of Spooner's theory; however, the condition of the lora and labium, the structure of the mandibular levers, the absence of a distinct anteclypeus, and the presence of maxillary levers and cephalic glands all tend to support China's

hypothesis. The several resemblances between *Gelastocoris* and the naucorid *Pelocoris* are interesting in view of China's (1955b) proposal that the Naucoridae are the most generalized of the totally aquatic families.

The structure of the food pump of *Gelastocoris* is worthy of some discussion. The very thorough studies of Marks (1958 and 1959) make it possible to compare this structure with that of several aquatic Heteroptera. Unfortunately, no similar study has been made of the food pumps of the semi-aquatic forms, so that no comparisons can be made with those families.

Marks found a relatively simple pump in *Ranatra* and *Belostoma* and a more complicated one in *Hesperocorixa, Pelocoris,* and *Notonecta.* The resemblances between *Gelastocoris* and the last two forms are rather marked. Marks' diagrams (1959, Figs. 2, 4) of lateral views of the pumps of *Pelocoris* and *Notonecta* show them to be very similar to that of *Gelastocoris* in general shape, and to possess certain epipharyngeal specializations in the same region in which the gelastocorid striated plates occur. These specializations consist of two heavily sclerotized, tooth-bearing transverse bars, one on either side, which, like the striated plates, are joined at the midline. At the point of junction are tendons for muscle attachment, similar to those of Group 3 in *Gelastocoris. Notonecta* possesses a second pair of bars anterior to these, while *Pelocoris* has a series of toothed folds concealed beneath the transverse bars. Marks proposed that these epipharyngeal elaborations are straining or filtering devices, as may be the case in *Gelastocoris.*

Whether or not the striated plates can be homologized with the transverse epipharyngeal bars of *Pelocoris* or *Notonecta* is a matter of conjecture. It is difficult to imagine how either could have developed from the other, although it is possible that the striated plates could have arisen from the bars plus the tooth-bearing folds of *Pelocoris.* It seems more likely, however, that both the bars and the striated plates, if homologous, developed from an intermediate ancestral condition. Marks (1959) was uncertain as to whether the transverse bars of *Pelocoris* are homologous with those of *Notonecta.* He stated that although the similarities between them are very great, the muscles activating the bars of *Notonecta* are cibarial in origin (anterior to the

frontal ganglion), while those of *Pelocoris* are pharyngeal (posterior to the frontal ganglion).

While considering this question, the author dissected food pumps of both *Notonecta* and *Pelocoris* and found that in the latter the frontal ganglion is located much farther posteriorly than Marks described it. It is in exactly the same position, relative to the muscles of the pump, as that of *Gelastocoris;* only a few thin strands of muscle (from the posterior portion of Marks' Muscle Group 3) lie posterior to the ganglion, the rest being anterior to it. Therefore, most of the *Pelocoris* pump is, like that of *Gelastocoris,* cibarial in nature, and consequently it appears quite probable that the transverse bars of *Pelocoris* and *Notonecta* are homologous. The great similarity between the musculature of the food pumps of *Pelocoris* and *Gelastocoris* makes it possible to suggest the probable muscle homologies which were listed earlier. Mm. dilatores cibarii primus and secundus of *Gelastocoris* seem to correspond to Marks' Muscle Group 1, and M. dilator cibarii tertius, activating the striated plates, probably represents Marks' Muscle Group 2, which moves the transverse bars. M. dilator cibarii quartius resembles Marks' Muscle Group 3; in both insects, the frontal ganglion is found within this muscle group.

Although the resemblances between the food pumps of *Gelastocoris* and *Pelocoris* are strong enough to suggest these few homologies, the author will not attempt to make similar comparisons between *Gelastocoris* and the other aquatic bugs, since the relationships between the groups studied by Marks are not clear. The reader is referred to that author's two excellent papers (1958 and 1959) for a complete discussion of this problem.

One of the chief obstacles encountered by Marks in his attempt to homologize the parts of the food pumps in different aquatic bugs was the position of the frontal ganglion in relation to the various muscle groups. In the author's opinion, too much emphasis has been placed on the distinction between cibarial and pharyngeal muscles. The origins and insertions of these two groups of muscles have been used by Snodgrass (1947) and many other authors as criteria not only for distinguishing the cibarial from the pharyngeal portions of the food pump but for determining the boundary between the frons and the clypeus. DuPorte (1946), in discussing the facial sclerites, pointed out that

the origins of the pharyngeal or cibarial muscles might easily shift from one sclerite to another, and Ferris (1944) has expressed a similar opinion. It seems possible that the insertions of such muscles could also shift — that muscles posterior to the frontal ganglion could come to insert on a cibarial portion of the food pump, or that cibarial muscles might shift their insertions to the pharyngeal portion. In the insects studied by Marks, the frontal ganglion varies, in its position relative to the muscles, from one species to the next. It may be that these differences are not significant but, as Marks (1959) has suggested, can be explained by muscle shifts.

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ABBREVIATIONS USED IN FIGURES

A – antenna
AD – afferent salivary duct
AF – anteriormost portion of hypopharynx of food pump
AM – articular membrane of antenna
B – brain (cut edge)
BL – base of first labial segment
C – clypeus
CE – compound eye
CN – clypeal connectives
CO – orifice of cephalic gland
CR – cranial exoskeleton (cut edge)
D – dorsal suture
DG – dorsal wall of genal sac
DH – dorsal surface of hypopharyngeal wing
E – epipharynx of food pump
ED – efferent salivary duct
EP – epipharyngeal projection
ER – epipharyngeal ridge
F – food pump
FC – food canal
FG – frontal ganglion (cut edge)
G – gula
G1 – tendons of Group 1
G2 – tendons of Group 2

G3 – tendons of Group 3
G4 – tendons of Group 4
GL – gular lobe
H – hypopharynx of food pump
HF – hypopharyngeal flap
HW – hypopharyngeal wing
IM – intersegmental membrane
IS – intersegmental sclerite between third and fourth labial segments
L – labium
LA – lateral apodeme
LI – first labial segment
LII – second labial segment
LIII – third labial segment
LIV – fourth labial segment
LB – labrum
LF – lumen of food pump
LO – lorum
MD – mandibular stylet
MDL – mandibular lever
MG – medial wall of genal sac
MX – maxillary stylet
MXL – maxillary lever
MXP – maxillary plate
O – ocellus
OC – occipital condyle
OF – occipital foramen
OP – oblique plate
OV – oval raised area on epipharyngeal plate
P – postocciput
PA – pedicel (second antennal segment)
PB – pigmented border of epipharynx
PL – epipharyngeal plate
PP – posterior pharynx
S – salivary pump
SA – scape (first antennal segment)
SC – salivary canal
SD – dorsal intersegmental sclerite between first and second labial segments
SE – subesophageal ganglion (cut edge)
SG – stylet groove
SP – striated plate
SU – suspensory plate
SV – ventral intersegmental sclerite between first and second labial segments
T – transparent area in hypopharynx of food pump
TA – tendon for M. depressor scapi
TM – tendon for M. retractor setae mandibularis secundus
TS – tendon for M. retractor pistilli
U – U-shaped ridge on cranium
V – ventral suture
VG – ventral wall of genal sac
VH – ventral surface of hypopharyngeal wing
VX – vertex
1 – M. levator labii
2 – M. depressor labii primus
3 – M. transversalis labii primus
4 – M. depressor labii secundus
5 – M. transversalis labii secundus
6 – M. transversalis labii tertius
7 – M. retractor segmenti ultimi labii
8 – M. protractor setae mandibularis primus
9 – M. protractor setae mandibularis secundus
10 – M. retractor setae mandibularis primus
11 – M. retractor setae mandibularis secundus
12 – M. protractor setae maxillaris
13 – M. retractor setae maxillaris
14 – M. dilator cibarii primus
15 – M. dilator cibarii secundus
16 – M. dilator cibarii tertius
17 – M. dilator cibarii quartius
17A – M. dilator praepharyngis
18 – M. dilator postpharyngis ventralis
19 – M. dilator postpharyngis dorsalis
20 – M. levator scapi
21 – M. depressor scapi
22 – M. scapo-pedicellaris medialis
23 – M. scapo-pedicellaris lateralis
24 – M. dilator oris glandulae capitis
25 – M. retractor pistilli

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By Marion Grey

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No. 2 — *A Preliminary Review of the Family Gonostomatidae, with a Key to the Genera and the Description of a New Species from the Tropical Pacific.*

By Marion Grey

In recent years collections made aboard the research vessel *Oregon* of the United States Fish and Wildlife Service, have yielded a number of species of the family Gonostomatidae. Among these were the first known western Atlantic specimens of the genera *Triplophos* and *Argyripnus;* a new maurolicid genus and species, *Sonoda megalophthalma* Grey (1959); new and well preserved material of *Yarrella blackfordi* Goode and Bean, and *Polymetme corythaeola* (Alcock); and adult specimens of *Diplophos maderensis* (Johnson). A study of these specimens, preparatory to a revision of the family Gonostomatidae, has resulted in the following discoveries.

1. *Yarrella blackfordi* possesses serial photophores on the body other than the ventral and lateral rows described on the types, and therefore all species presently placed in the genus *Yarrella* Goode and Bean, except the type species, must be excluded from the genus.

2. *Lychnopoles* Garman is a synonym of *Yarrella.*

3. The genus *Polymetme* McCulloch, usually considered a synonym of *Yarrella,* is reinstated to include most of the species formerly placed in the latter.

4. *Yarrella mauli* Poll has been assigned to a new genus, *Pollichthys* (Grey, 1959).

5. *Manducus* Goode and Bean is reduced to the status of a subgenus of *Diplophos* Günther.

Other material studied has produced the following results.

1. *Photichthys nonsuchae* Beebe has been placed in a new genus, *Woodsia,* and a second specimen of this species has been described from the eastern Pacific (Grey, 1959).

2. *Snellius* Koumans is a synonym of *Margrethia* Jespersen and Tåning.

3. *Gonostoma atlanticum* Norman, which was first described as a subspecies of *G. denudatum* Rafinesque, is given specific rank.

4. A new species of the genus *Gonostoma* Günther is described from the Pacific, and new records of *G. gracile* Günther are listed.

5. New material of *Danaphos* Bruun from the eastern Pacific has shown that *D. asteroscopus* Bruun is probably a synonym of *D. oculatus* (Garman).

To the following people I would like to express my appreciation for the loan of specimens, or for information or advice. Dr. Frederick H. Berry, Dr. Henry B. Bigelow, Mr. Harvey R. Bullis Jr., Dr. Daniel M. Cohen, Mrs. Myvanwy Dick, Dr. Alfred W. Ebeling, Dr. Carl L. Hubbs, Dr. Einar Koefoed, Mr. G. E. Maul, Dr. Giles W. Mead, Dr. James E. Morrow Jr., Dr. George S. Myers (in particular), Dr. Max Poll, Dr. Andreas B. Rechnitzer, Prof. L. R. Richardson, Dr. C. Richard Robins, Dr. L. P. Schultz, Miss Margaret Storey, and Dr. D. W. Tucker.

I am indebted to Dr. Rainer Zangerl for a number of X-ray photographs, which made possible vertebral counts of most of the species studied, and to Miss Janet Wright for assistance in the preparation of Figure 3. Figure 1 was drawn by Mrs. Myvanwy Dick and Figure 2 by Mr. John Pfiffner, Staff Artist, Chicago Natural History Museum.

In spite of recent discoveries the inter-relationships of gonostomatid genera are still obscure, and a separation into subfamilies has not been attempted. The maurolicid genera certainly form a natural group but it seems unnatural and misleading to lump the remaining genera in a single subfamily, and I cannot see any advantage in introducing four or five new subfamilies at this time. Future discoveries may make such division possible, as the sea undoubtedly harbours undiscovered species, but undiscovered species are more likely to close the gaps between the known ones.

The maurolicid genera, given family rank by some and subfamily rank by most authors, are distinct from other gonostomatids in having many of the photophores grouped together and connected to a common gland, as well as in having fewer photophores on the branchiostegal membranes. Maurolicid fishes usually differ further in having smaller mouths, minute teeth in the jaws, and well developed pseudobranchiae, but there are exceptions. The pseudobranchiae of *Sonoda* and *Danaphos,* for

example, are small, fragile, and not always discernible; and furthermore two non-maurolicid genera, *Margrethia* and *Diplophos* (subgenus *Diplophos*), also possess pseudobranchiae. Maurolicid genera show more variation among themselves in some characters than do other groups of gonostomatid genera, especially in the relative positions of the dorsal, anal and ventral fins.

The four genera *Gonostoma, Cyclothone, Bonapartia* and *Margrethia* also form a natural group, distinguished principally by the absence of photophores on the isthmus; and the genus *Ichthyococcus* is so aberrant that there would be little or no objection to placing it alone in a separate subfamily. However, attempts to join the remaining genera into natural groups have not been entirely successful. *Diplophos, Triplophos* and *Yarrella* appear to be related, sharing such characters as numerous rows of photophores on the body, a tendency toward a long premaxillary, and the absence of an adipose fin; and *Photichthys, Woodsia, Vinciguerria* and *Pollichthys* can be grouped together in their possession of two suborbital photophores. But *Polymetme* cannot be placed in either of these groups. In general appearance it is much like *Photichthys* but the resemblance is relatively superficial. In its dentition and rather long premaxillary *Polymetme* approaches *Yarrella* but in the arrangement of the photophores, meristic characters, and the presence of an adipose fin it is similar to *Pollichthys*. *Polymetme* also has a tendency toward the elongation of some of the photophores, a character usually associated with the maurolicid genera. Some genera have one or two common characters although they do not seem to be otherwise closely related. For example, *Danaphos* and *Triplophos* are the only members of the family in which the dorsal origin is more than slightly in advance of the middle of the body length; and tubular eyes are found in *Ichthyococcus,* young *Vinciguerria, Valenciennellus,* and *Danaphos.*

Generic relationships have been tentatively arranged as shown in Figure 1. It is impossible to state which genus is the most primitive but it is possibly either *Diplophos* or *Yarrella.* Rechnitzer and Böhlke (1958, p. 15) have written of the evolutionary trend of the family Sternoptychidae (subfamilies Gonostomatinae, Maurolicinae, Sternoptychinae): ". . . the body becomes deep and foreshortened, with an enlarged head region and with

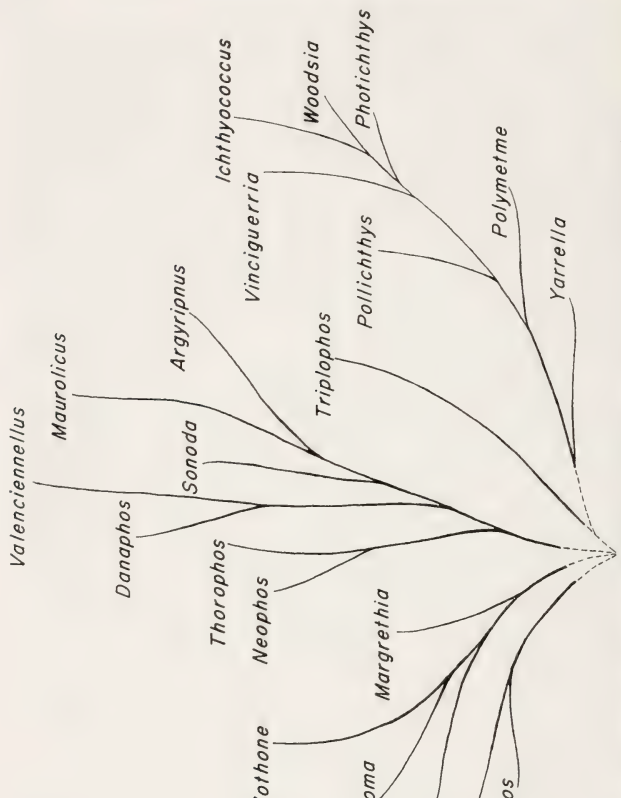

Figure 1. Diagram showing possible relationships of genera of the family Gonostomatidae.

a reduced number of segmental structures. The interruption of the anal photophores [i.e., their separation into groups] is in the same line of evolution, and the out-of-line arrangement of the anterior ventral photophores is an obvious specialization. An enlargement of the photophores, especially in the vertical axis, marks both the species [*Ichthyococcus*] sequence and the subfamily sequence." Such trends were demonstrated by these authors in the genus *Ichthyococcus*, with *elongatus* Imai the most primitive of three species and *irregularis* Rechnitzer and Böhlke the most advanced. A similar trend is evident within the genera *Diplophos* and *Yarrella* but on the whole the genera of the family Gonostomatidae, including maurolicids, cannot be fitted into such an evolutionary picture with any feeling of confidence. It is possible to trace a progression from *Diplophos* to *Ichthyococcus* through the following genera: *Yarrella* → *Polymetme* → *Pollichthys* → *Photichthys* → *Vinciguerria* → *Woodsia*, but in the remaining groups of genera there may be more than one line of evolution and these are obscure at best. *Gonostoma* and *Bonapartia* are obviously closely related, as are *Gonostoma* and *Cyclothone*, but *Margrethia*, which is the only short and deep-bodied member of this group, shows relationship to all three of the other genera without a strong resemblance to any of them. As for the maurolicid genera, even after disposing of *Argyripnus* as an aberrant offshoot, we are left with six genera which defy any kind of orderly arrangement from primitive to specialized or advanced except that *Maurolicus* does have a short, deep body and a relatively low vertebral count and could therefore possibly be considered the most specialized. And *Neophos*, having fewer of the photophores in groups, a large mouth, and an elongate body, is probably the most primitive (its vertebral count is not known). In Figure 1 the maurolicid genera have been placed near *Diplophos*, *Margrethia* and *Triplophos* for the following reasons.

1. According to Brauer (1908, p. 27) the photophore structure of *Triplophos* is very similar to that of maurolicids.

2. *Margrethia* is similar in several respects to maurolicids (pseudobranchiae present, some of the photophores elongated and close together) and there is further evidence also that maurolicids stem from something near the *Gonostoma-Margrethia*

group of genera. In both groups the distance between the ventral bases and the anal origin is short and the VAV count is correspondingly low (with the exception of the newly discovered *Gonostoma ebelingi*, which has 10 VAV and a rather long space between ventrals and anal). And in both there is a tendency toward a more anteriorly situated anus than in most other gonostomatids.

3. *Diplophos* and the maurolicid group show a possible common origin in the possession of pseudobranchiae (subgenus *Diplophos*) and in having the spines on the inner edge of the first gill arch absent or reduced to rudiments. These spines are well developed, even though usually short, in all other gonostomatids, and it may be significant that they are minute in *Ichthyococcus, Bonapartia* and *Margrethia*. It is also interesting to note that in some specimens of *Diplophos* (subgenus *Diplophos*) the rows of minute photophores found below the eye and along the lower jaw appear to be contained in a common black membrane, although I am unable to assert that this structure is similar to the connective membrane of the photophores of maurolicids.

Of the twenty genera included in the family Gonostomatidae at least nine are monotypic and it is sometimes difficult to judge whether differences between species are generic or specific. However, where several species of a genus are known the interspecific differences are usually slight and the existence of numerous genera seems to be natural. *Diplophos, Yarrella* and, especially, *Gonostoma* are exceptional in having more or less sharply differentiated species. A number of characters seem to be highly plastic throughout the family and even sometimes within a genus. There are also areas of stability but these are notable for their exceptions, as can be seen by the following examples.

1. Until recently all described maurolicid genera had only 4-6 VAV photophores; and no known species of *Gonostoma* had more than 5. However, the recently described maurolicid, *Sonoda megalophthalma*, has a VAV count of 7-8; and the newly discovered *Gonostoma ebelingi* has 10 VAV photophores.

2. In all genera except some maurolicids and *Ichthyococcus* the ventral fins are inserted in advance of the dorsal origin. They are behind the first dorsal ray in *Ichthyococcus* and are variable

in position in maurolicid genera (behind the dorsal origin in *Danaphos*, well ahead of it in *Neophos*, *Thorophos*, *Valenciennellus* and *Sonoda*, and close to a vertical from the first dorsal ray in *Argyripnus* and *Maurolicus*).

3. The dorsal origin in non-maurolicid genera is in advance of the anal origin in all but *Gonostoma*, *Cyclothone* and *Bonapartia*. In these three genera either the dorsal and anal origins are opposite one another or the anal is farther forward, but in *Margrethia*, the fourth member of this group, the dorsal origin is always slightly in front of the anal origin. In maurolicid genera, again, the relative positions of these fins is variable (dorsal origin anterior to anal origin in *Argyripnus*, *Danaphos* and *Maurolicus*, opposite or behind it in *Sonoda*, *Valenciennellus*, *Thorophos* and *Neophos*).

4. The presence or absence of an adipose fin is a reliable generic character except in *Gonostoma*, in which this fin is present in all but two species, *atlanticum* and *gracile*. It is also very small and difficult to distinguish in several maurolicid genera.

5. In general the anus is situated close to the origin of the anal fin in non-maurolicid genera and more remote from it in maurolicids. Again there are exceptions, for the anus is situated well in advance of the anal origin in the genus *Cyclothone* and in two species of *Gonostoma* (*ebelingi*, *gracile*); and it is near the anal fin in three maurolicid genera (*Neophos*, *Valenciennellus*, *Maurolicus*).

6. The mouth is large and oblique in all non-maurolicid genera excepting *Ichthyococcus*, in which it is relatively small. Three maurolicids also have large, oblique mouths (*Neophos*, *Thorophos*, *Argyripnus*) but in *Danaphos*, *Valenciennellus*, *Sonoda* and *Maurolicus* the mouth is relatively small and the gape very oblique or almost vertical.

7. The extent to which the premaxillary enters the gape varies in the extreme, being excluded from it in *Ichthyococcus* and forming virtually all of it in *Triplophos*. In maurolicid genera the premaxillary is always at least half as long as the toothed portion of the maxillary and is usually more than half as long. The premaxillary of *Diplophos* and *Yarrella* is equal to or longer than the toothed portion of the maxillary; in *Polymetme* it is only slightly shorter; in *Pollichthys*, *Photichthys* and *Woodsia*

it is about half, or more than half as long; and in *Vinciguerria, Bonapartia, Margrethia, Gonostoma* and *Cyclothone* it is less than half as long.

8. The premaxillary teeth are uniserial in all gonostomatids excepting *Yarrella, Triplophos* and *Polymetme*, in which they are in two rows, and *Neophos*, in which they are arranged irregularly. Maxillary teeth are always uniserial as far as known, although in some species one or two of the most posterior maxillary teeth may be situated higher than the remainder. The lower jaw teeth also are mostly in a single row except anteriorly, where there is usually a very short outer row of teeth. However, in some genera the teeth on the mandible are biserial for almost its full length (*Yarrella, Triplophos, Polymetme, Argyripnus*), or for about half its length (*Vinciguerria, Sonoda*); and in *Ichthyococcus*, probably *Valenciennellus*, and sometimes *Maurolicus*, they are entirely uniserial and lack the anterior outer row. The mandibular teeth of *Danaphos* are irregular anteriorly and uniserial posteriorly.

9. Teeth on the vomer, palatines, pterygoids and tongue, when present, are usually small or even minute, although *Gonostoma bathyphilum* has a few much enlarged pterygoid teeth posteriorly. *Cyclothone* may have as many as five or six small, close-set teeth in a lengthwise row on each side of the vomer (absent in at least one species), and in this genus the palatine and pterygoid teeth are present only on the anterior ends of the bones, in small clusters. Other genera have fewer vomerine teeth in crosswise rows (or none); the palatine teeth, if present, are linear; and the pterygoid teeth, if present, are arranged in more or less circular patches of minute teeth with sometimes an irregular, sparse row posteriorly. *Maurolicus* sometimes has a few pterygoid teeth but these are apparently lacking in all other maurolicid genera. Only three non-maurolicid genera lack pterygoid teeth (*Ichthyococcus, Vinciguerria, Woodsia*) but they are sometimes absent also in *Diplophos* (subgenus *Diplophos*), *Triplophos, Pollichthys* and *Photichthys;* and are microscopic in *Yarrella*, if present at all. Teeth have been found on the tongue only in *Diplophos* (sometimes), *Pollichthys, Photichthys* (sometimes), *Bonapartia, Margrethia,* and in two species of *Gonostoma* (*denudatum, atlanticum* rarely).

10. Meristic characters are shown in Table 6.

The key on page 69 has been based on all known genera except *Thorophos* Bruun, of which no specimens have been seen; nor have I seen any Indian or Pacific Ocean material of *Triplophos*, *Polymetme*, *Vinciguerria*, *Ichthyococcus*, *Margrethia*, *Argyripnus* or *Valenciennellus*. It should be emphasized also that the genus *Cyclothone* has not yet been studied in detail. The following hitherto unreported material has been examined but is not pertinent to the present publication except as it applies to the characters contained in the key to the genera.

Photichthys argenteus Hutton. Three specimens, standard length 100-118 mm., off Cape Palliser, Cook Strait, New Zealand, 1942, from the stomach of a groper caught in 40-50 fathoms (73-91 meters). Received from Prof. L. R. Richardson, Victoria University College, Wellington, New Zealand. The genus *Photichthys* is defined on page 100.

Ichthyococcus Bonaparte. Only a few small specimens of *I. ovatus* (Cocco) are available for study (Grey, 1955, p. 273). Included in this lot are three hitherto unrecorded metamorphosing specimens. The premaxillary bones are very difficult to distinguish on specimens of *I. ovatus* but a communication received from Dr. A. B. Rechnitzer (1958, *in litt.*) has confirmed the impression that the premaxillary is excluded from the gape. Dr. Rechnitzer also found it difficult to distinguish these bones on two eastern Atlantic specimens of *I. ovatus*, but an examination of three larger specimens of *I. elongatus* Imai revealed that the premaxillary terminates at the apex of the inverted V-shaped symphysis of the upper jaw; and that the maxillary is continuous throughout the gape and is toothed, or serrated, along its entire edge.

Gonostoma Rafinesque 1810. A few unrecorded western Atlantic specimens of *G. elongatum* Günther 1878 and *G. bathyphilum* (Vaillant) 1888, from the collection of the United States National Museum, have been examined, as well as new material of *G. elongatum* from the Gulf of Mexico, the Caribbean Sea, and off northern South America (*Oregon*). The genus is defined on page 102, new material of *G. atlanticum* Norman from both the Atlantic and Pacific oceans is described on page 106,

and a new species, *G. ebelingi*, from the tropical Pacific, is described on page 109. I have also seen two Mediterranean specimens of *G. denudatum* Rafinesque 1810, loaned by the Museum of Comparative Zoology, and the following unrecorded specimens of *G. gracile* Günther 1878, most of them loaned by Scripps Institution of Oceanography. The latter show that *G. gracile* has a wide distribution in the northern and western Pacific.

Western Pacific: Five, standard length 60-110 mm., C.N.H.M. No. 42780, taken during the *Albatross* Philippine cruise off Hong Kong, China, 6 November 1908; eleven, standard length 40-119 mm., SIO No. H 53-367, Kii Strait, Japan, 23-24 October 1952, 10′ midwater trawl, depth not known; one, standard length 95 mm., SIO No. H 51-371, Japan Trench, 32° 08′ N., 142° 04′ E., 26 October 1953, *S. F. Baird*, 10′ midwater trawl, 0-4455 fathoms (0-8147 meters); five, standard length 71-121 mm., SIO No. H 53-356, off Honshu, Japan, 35° 01.8′ N., 145° 12′ E. to 34° 48.5′ N., 145° 05.4′ E., 1 October 1953, *S. F. Baird*, 10′ midwater trawl, 1000 fathoms (1829 meters).

North and middle Pacific: Three, standard length 69-87 mm., SIO No. H 53-335, southeast of Kamchatka, 51° 09.5′ N., 164° 32.6′ E. to 50° 59.3′ N., 164° 27.1′ E., 4 September 1953, *S. F. Baird*, 10′ midwater trawl, 0-580 fathoms (0-1061 meters); one, standard length *ca.* 83 mm., SIO No. H 53-344, off the Kurile Islands, 45° 29.7′ N., 154° 20′ E. to 45° 18.8′ N., 154° 02.6′ E., 16 September 1953, *S. F. Baird*, 10′ midwater trawl, 0-2600 fathoms (0-4755 meters); one, standard length *ca.* 92 mm., SIO No. H 53-371, 48° 58.3′–37.4′ N., 157° 49.8′–29′ W., 5-6 September 1951, *Horizon*, 10′ midwater trawl, 2200-2400 fathoms (4023-4389 meters); four, standard length 105-116 mm., SIO No. H 51-374, 37° 29′–01.5′ N., 154° 03.5′–153° 58.2′ W., 12-13 September 1951, *Horizon*, 10′ midwater trawl, 700 fathoms (1280 meters); three, standard length 96.5-111.5 mm., SIO No. H 51-360, 43° 08′ N., 150° W., 13 August 1951, 10′ midwater trawl, 35-175 meters; three, standard length 102-120 mm., SIO No. H 51-375, 31° 54.3′ N., 152° 21.6′ W. to 31° 36.5′ N., 152° 03.6′ W., 15 September 1951, *Horizon*, 10′ midwater trawl, 1790 fathoms (3274 meters); one, standard length 96 mm., SIO No. H 53-312, 44° 59′ N., 148° 46.5′ W., 4 August 1953, *S. F. Baird*, 1 meter plankton net, 0-1000 fathoms (0-1829 meters); five, standard

length 107-130 mm., SIO No. H 51-358, 40° 35′ N., 147° 55′ W., 10 August 1951, *Horizon*, 10′ midwater trawl, 350-600 meters; one, standard length 116.5 mm., SIO No. H 53-308, 39° 23′ N., 142° 51′ W. to 39° 15.5′ N., 142° 54.9′ W., 1 August 1953, *S. F. Baird*, diving dredge No. 1 (no depth).

Bonapartia pedaliota Goode and Bean 1895. One specimen, standard length 42 mm., U.S.N.M. No. 108303, *Caroline*, Virgin Islands, 18° 44′ N., 65° 15′ 15″ W., 26 February 1933, 600 fathoms (1097 meters).

Margrethia Jespersen and Tåning 1919. Koumans (1953, p. 183) was apparently unaware of the description of the genus *Margrethia* when he proposed the genus *Snellius*, which is an obvious synonym of *Margrethia*.

Argyripnus atlanticus Maul 1952. One specimen, standard length 67 mm., *Oregon*, September 1957, Caribbean Sea, further data lost. The type of *atlanticus* was described and figured as having four OP and was said to differ from *ephippiatus* Gilbert and Cramer 1896 and *iridescens* McCulloch 1926 in having a much larger posterior opercular organ. Both Pacific species were also described as having two photophores in this area: ". . . one above the other and separated by a black, metallic-hued space" (McCulloch, 1926, p. 170); ". . . one above the other, at the two ends of a short vertical steel-blue band . . ." (Gilbert and Cramer, 1896, p. 415). In the specimen examined the opercular organ has the outward appearance of a single, greatly elongated and enlarged one encased in a deep black sheath, with a luminous area exposed near the top. Actually there probably are two organs involved, but they are at least encased in a common sheath, and the structure is similar in all species, as can be seen in the published figures.

Danaphos Bruun 1931. The genus is defined on page 112 from new material in the collection of Scripps Institution of Oceanography.

Neophos Myers 1932. The type has been examined and the genus is defined on page 114.

Valenciennellus tripunctulatus (Esmark) 1870. One specimen, 30.5 mm., Stanford University No. 18713, *Oregon* Station 841, Gulf of Mexico, 25° 58′ N., 88° 00′ W., 6 October 1953, 830-930 fathoms (1518-1700 meters), reported as *Maurolicus müller*i

by Springer and Bullis (1956). The genus *Valenciennellus* Jordan and Evermann contains two, and possibly three species. *V. tripunctulatus*, of which *V. stellatus* Garman 1899 is possibly a synonym, is cosmopolitan in tropical and subtropical waters. *V. carlsbergi* Bruun 1931 has been found only in the tropical Indo-Malayan area. The latter differs from *tripunctulatus* in having a shorter and deeper caudal peduncle, only two OA photophores, and only three groups of AC photophores (a group of three above the tenth to twelfth anal rays, a group of two above the middle of the anal fin, and a group of four on the caudal peduncle).

V. stellatus was distinguished by Garman (1899, p. 239) from *V. tripunctulatus* by two characters, a shorter dorsal fin and a smaller number of AC photophore groups. Actually, however, the dorsal count of *stellatus* is higher, numbering twelve rays instead of the seven to ten of *tripunctulatus*. Garman's conclusion that the dorsal fins of the two species differed was based on an error in the figure published by Lütken (1892, pl. 1, fig. 6). This figure shows a long dorsal fin of about seventeen rays although in the text Lütken gave the dorsal count as nine or ten rays. The error in the figure probably resulted from the artist having drawn the dorsal and the adipose as a continuous fin. Garman's second distinction, the presence of only four groups of AC photophores, may be valid. There is, however, variation in the number of AC groups in *tripunctulatus*, although five is the typical number. Only examination of a series of specimens from the eastern Pacific will show with certainty whether or not *stellatus* is a distinct species with a constantly higher number of dorsal rays and a lower number of AC photophores.

It should be noted that Jespersen's description (1933) of the photophores of *V. tripunctulatus* is misleading in part. His OA count of 10 includes the second IV group of (4) and the lower posterior OP. His "series of 4 organs underneath the cheek" refers to the BR (six in Jespersen's figure), which are visible beneath the transparent jaw bones in most specimens. Finally, the "two or three on the branchiostegal membrane" must refer to the first IV group of (3) on the isthmus.

Maurolicus muelleri (Gmelin) 1789. A few unreported specimens from the collection of the United States National Museum

have been examined, four of them washed ashore on the Massachusetts coast and two found on the beach at Juan Fernandez in the southeastern Pacific.

In the key, and in descriptions, the following symbols are used to represent the photophores: ORB, those situated close to the eye; OP, opercular photophores; SO, a pair often found near the symphysis of the lower jaw; BR, organs on the branchiostegal membranes; IV, pre-ventral photophores of the ventral series; VAV, those of the ventral series found between the ventral bases and the anal origin; AC, photophores of the ventral series posterior to the anal origin; IC, total number in the ventral series, from tip of isthmus to base of caudal; OA, photophores of the lateral series. Photophore counts in parentheses indicate that these organs are grouped in a common gland.

Key to the Genera and Subgenera of the Family Gonostomatidae

1a. BR 8 or more (reduced in size and number in *Cyclothone obscura*, obscure and very small in *Gonostoma bathyphilum*). Serial photophores separate, not grouped in common glands.

2a. Photophores present on isthmus. IV 20 or more. IC 42 or more. [Dorsal origin always in advance of anal origin. Body always with at least two rows of serial photophores].

3a. More than two rows of photophores on body, those above the IC and OA frequently mostly or entirely lost with the skin. No adipose fin. OA 40 or more. [ORB 1, close to front of eye or below it].

4a. Teeth of upper jaw all uniserial. Teeth of lower jaw uniserial except for a short outer row anteriorly. On posterior half of lower jaw a row of minute photophores in adult, preceded by a somewhat larger photophore. Lateral line area with a row of small photophores extending on to caudal fin (often partially lost). Gill rakers on lower limb of first arch 7-9. Vertebrae 63 to *ca.* 85 (and more?).

Diplophos Günther 1873
Atlantic, Pacific, Indian

5a. Dorsal origin about in middle of body, usually slightly nearer tip of snout than caudal base. Head and trunk approximately same length as tail, distance between snout and anal origin *ca.* 47.5-51.2%, and between anal origin and caudal base *ca.* 48.0-53.0% of standard length. Depth 8.2-12.3% of standard length. Anal rays (43?) 53-68. IV 40-49. AC 43-49. IC 97-113. OA 66-87. Lateral line *ca.* 80-98. Vertebrae *ca.* 85 (and more?).

subgenus *Diplophos* Günther 1873
Atlantic, Pacific, Indian

5b. Dorsal origin slightly behind middle of body (close to middle in young). Head and trunk longer than tail (proportionately less so in young), distance between snout and anal origin 59.0-63.0%, and between anal origin and caudal base 36.5-41.2% of standard length. Depth *ca.* 15-17% of standard length. Anal rays 36-41. IV 30-32. AC 28-30. IC 70-75. OA 44-48. Lateral line 63-68. Vertebrae 63.

subgenus *Manducus* Goode and Bean 1895
Atlantic

4b. Teeth of premaxillary biserial. Teeth of lower jaw biserial on most of its length. No photophores on posterior half of lower jaw. Lateral line area not marked by a row of photophores. Gill rakers on lower limb of first arch 12-16. Vertebrae 45 to *ca.* 60(?).

6a. Trunk much shorter than tail. Dorsal origin far in advance of middle of body length. Toothed portion of maxillary very short, scarcely entering gape. Snout shorter than eye. Dorsal 10-12, anal 54-63. VAV 5-7. AC 35-41. Head with additional photophores above upper jaw. Vertebrae *ca.* 60?

Triplophos Brauer 1902
Atlantic, Indian

6b. Trunk slightly longer than tail. Dorsal origin about in middle of body length or slightly behind it. Toothed portion of maxillary entering gape. Snout longer than eye. Dorsal 14-16, anal 26-31. VAV 9-12. AC 20-27. Photophores on upper part of head consisting only of the ORB and OP. Vertebrae 45-54.

Yarrella Goode and Bean 1895
Atlantic, Pacific

3b. Body with only two rows of photophores. Adipose fin present. OA 16-34.

7a. ORB 1, close to front of eye. Premaxillary teeth biserial. AC 22-25. [Vertebrae 45].

Polymetme McCulloch 1926
Atlantic, Pacific, Indian

7b. ORB 2, one close to front of eye, one close to its hind margin or below center (*Ichthyococcus*). Teeth of upper jaw all uniserial. AC 12-21.

8a. Eye normal (except somewhat tubular in some juvenile *Vinciguerria*). Mouth large, bordered by premaxillary anteriorly. Jaws equal, or lower jaw projecting slightly beyond upper jaw anteriorly. Teeth relatively well developed. Ventral fins in advance of dorsal origin. Gill rakers minutely denticulate on inner edge.

9a. Anal origin beneath dorsal or close behind a vertical from its last ray. Branchiostegal rays 9-13. BR 8-9 (12?). OA 19-25.

10a. Anal origin beneath middle or anterior portion of dorsal. Anal 22-30. Anterior ORB larger than posterior one. AC 19-21. Vertebrae *ca.* 40?

Pollichthys Grey 1959
Atlantic, Pacific

10b. Anal origin beneath middle or end of dorsal. Anal 12-16. ORB equal in size or posterior one larger. AC 12-16. Vertebrae (36?) 38-42.

Vinciguerria Jordan and Evermann 1895
Atlantic, Pacific, Indian

9b. Anal origin well behind end of dorsal fin. Branchiostegal rays 17-21. BR 14-18. OA 29-34.

11a. Gill rakers normally developed, 11 + 4-5 on first arch. Premaxillary about half as long as toothed portion of maxillary. Body elongate, depth *ca.* 6-6.5 times in standard length. Anal 23-26. VAV 15-17. AC 16-18. OA 33-34, ending above anterior portion of anal fin. Vertebrae 51.

Photichthys Hutton 1872
Atlantic, Pacific

11b. Only 3-4 normally developed gill rakers at angle of first arch. Premaxillary more than half as long as toothed portion of maxillary. Body not elongate, depth *ca.* 5 times in standard length. Anal 14. VAV 11-12. AC 12. OA 29-31, ending above end of anal fin. Vertebrae? (myomeres *ca.* 45).

Woodsia Grey 1959
Atlantic, Pacific

8b. Eye tubular. Mouth small. Premaxillary not entering into gape. Lower jaw included anteriorly. Teeth minute. Ventral fins behind dorsal origin. Gill rakers short and smooth. [Anal origin well behind end of dorsal. Dorsal 10-15, anal 13-17. Branchiostegal rays 11-12. Lateral line 34-42. ORB 2. BR 11-12. IV 25-28. VAV 9-14. AC 12-14. OA 23-31. Vertebrae 38-47].

Ichthyococcus Bonaparte 1841
Atlantic, Pacific, Indian

2b. No photophores on isthmus. IV 17 or less. IC 26-43. [Premaxillary less than half as long as toothed portion of maxillary].

12a. Dorsal origin opposite or behind anal origin. No pseudobranchiae. SO present or absent.

13a. Body with at least two rows of photophores *or* photophores inconspicuous *or* obsolete. Dorsal 10-17. Pectoral 7-13. Adipose fin present or absent. Luminous glands usually present on procumbent caudal rays.

14a. Maxillary with a series of relatively long, slender teeth, and subequal, short teeth in the interspaces between them. Each palatine with a single row of teeth. Pterygoid teeth in a patch on each side anteriorly, these teeth small or minute; and a few teeth posteriorly, these sometimes enlarged. Vomer usually with one or two small teeth on each side, sometimes absent. Adipose fin present or absent. Anal rays 21-31. OA 11-21. SO present (except usually absent in *bathyphilum*). Vertebrae 37-40.

Gonostoma Rafinesque 1810
Atlantic, Pacific, Indian

14b. Maxillary teeth subequal, close-set, more or less increasing in size posteriorly, sometimes a few of them moderately enlarged. Palatine and pterygoid teeth usually present

anteriorly only, each in a small group of a few relatively prominent teeth; posterior pterygoid teeth, if present, microscopic. Vomer usually with a double row of several small, close-set teeth (absent, microscopic, or reduced to one or two in *braueri*, *alba* and *signata*). Adipose fin normally absent. Anal rays 16-21. OA 6-10. SO absent. Vertebrae 29-33.

Cyclothone Goode and Bean 1883
Atlantic, Pacific, Indian, Antarctic

13b. Body with a single row of conspicuous photophores. Dorsal 17-20. Pectoral 14-16. No adipose fin. No luminous glands on procumbent caudal rays. [SO present. Vertebrae 37].

Bonapartia Goode and Bean 1895
Atlantic

12b. Dorsal origin slightly in advance of anal origin. Pseudobranchiae present. SO absent. [Body with only one row of large, conspicuous, somewhat irregular photophores. Adipose fin present. Vertebrae 34].

Margrethia Jespersen and Tåning 1919
Atlantic, Pacific

1b. BR (6) or less (7 on one side of one specimen of *Sonoda*), conspicuous. At least some of the serial photophores grouped together in common glands appearing as black or silvery bands. [Photophores present on isthmus].

15a. AC composed largely of separate organs, more or less evenly spaced.

16a. Dorsal origin about in middle of body length, and a little behind anal origin. Ventral bases well ahead of dorsal origin. Eye normal. Dorsal 8-11. Anal 31-38. SO present.

17a. Photophores on isthmus, and VAV, in more than one group. AC 12-13, all single. OA 1. Dorsal 8. Anal 38. No adipose fin. Number of vertebrae unknown.

Neophos Myers 1932
Pacific

17b. Photophores on isthmus, and VAV, each in a single group. AC 14-15, mostly single but with a group of two anteriorly and another group of two just behind anal fin. OA 7. Dorsal 11. Anal 31. Adipose fin present. Number of vertebrae unknown.

Thorophos Bruun 1931
Pacific

16b. Dorsal origin well ahead of middle of body length and ahead of anal origin, which is behind end of dorsal fin. Ventral bases behind dorsal origin. Eye tubular. Dorsal 6. Anal 24-25. SO absent. [AC mostly single and rather widely and evenly spaced but with the first three in a group and a group of four on the peduncle, followed by a single organ. Vertebrae 38].

Danaphos Bruun 1931
Pacific, Indian

15b. AC composed of two to five groups of two or more organs each.

18a. Photophores between ventral and anal fins grouped separately from those above anterior portion of anal fin, the VAV straight and numbering 4-8.

19a. Dorsal origin about in middle of body length. Anal origin beneath or slightly in advance of dorsal origin. Ventral bases well ahead of dorsal origin. Trunk shorter than tail. SO absent. OA 7 or less.

20a. AC in three to six well separated groups of only two to four organs each. IV 20-24. VAV 4-5. AC 9-15. IC 36-40. Adipose fin present. Eye sometimes slightly tubular. Vertebrae 32-33?

Valenciennellus Jordan and Evermann 1895
Atlantic, Pacific, Indian

20b. AC in two subequal groups, each with sixteen organs or more. IV 16. VAV 7-8. AC 36-42. IC 58-66. No adipose fin. Eye normal. Vertebrae 40.

Sonoda Grey 1959
Atlantic

19b. Dorsal origin behind middle of body length. Anal origin behind dorsal origin. Ventral bases close to a vertical from first dorsal ray. Trunk longer than tail. SO present. OA 9. [AC in two long groups, preceded by a single elevated organ. Adipose fin present. Eye normal. Vertebrae 32-33].

Maurolicus Cocco 1838
Atlantic, Pacific, Indian

18b. Photophores between ventral and anal fins continuous with those above anterior portion of anal fin, this group rather sinuous and numbering 19-28, followed on the tail by one group of 5 and a second group of 12-18 organs. [Dorsal origin in advance of

anal origin. Ventral bases close to a vertical from first dorsal ray. Eye normal. SO absent. IC 53-67. Vertebrae 47].

Argyripnus Gilbert and Cramer 1896
Atlantic, Pacific

Diplophos Günther 1873

Diplophos Günther, 1873, Jour. Mus. Godeffroy, **2:** 101, type species *Diplophos taenia* Günther 1873, Atlantic, 22° N., 30° W. and 30° S., 24° W.; 1889, Rep. Sci. Res. Voy. Challenger, Zool., **31:** 32; Goode and Bean, 1895, Ocean. Ichth., p. 104; Barnard, 1925, Ann. So. Afr. Mus., **21:** 148; Norman, 1930, Discovery Rep., **2:** 295; Parr, 1931, Bull. Bingham Oceanogr. Coll., **2,** (4): 11 (part, *Lychnopoles* in synonymy); Fowler, 1936, Bull. Amer. Mus. Nat. Hist., **70:** 235; Matsubara, 1940, Suisan Kenkiu-shi, **35:** 319; Smith, 1949, Sea Fishes So. Afr., p. 105.

Manducus Goode and Bean, 1895, Ocean. Ichth., p. 514, type species *Gonostoma maderense* Johnson 1890, Madeira; Norman, 1930, Discovery Rep., **2:** 293 (part, *Lychnopoles* in synonymy); Fowler, 1936, Bull. Amer. Mus. Nat. Hist., **70:** 221, 1202 (part, *Lychnopoles* in synonymy).

Paraphotichthys Whitley, 1931, Australian Zool., **6:** 334, *Manducus* considered preoccupied by *Manduca* Huebner, *ca.* 1806, Lepidoptera.

Generic characters. Eye normal, moderate. Snout longer than orbit. Interorbital width at center of eye about equal to, or slightly greater than, diameter of orbit. Mouth large, oblique; edge of premaxillary straight; toothed edge of maxillary slightly convex; maxillary nearly reaching preopercle. Premaxillary almost, or quite as long as toothed edge of maxillary. Angle of preopercle slightly acute or nearly vertical. Teeth of upper jaw uniserial, unequal. Teeth of lower jaw unequal, uniserial except for a short outer row anteriorly. Vomer toothless or with 1-5 teeth on each side. Palatines each with a row of small teeth. Pterygoids with or without a patch of minute teeth on each side. Tongue with or without teeth. Gill rakers 7-9 + 3-5 = 10-14 on first arch. Spines on inner edge of first gill arch rudimentary or absent. Pseudobranchiae present or absent. Anus close to anal fin. Relative proportions of head and trunk to tail variable. Origin of dorsal fin near middle of body length, sometimes slightly before or slightly behind it. Origin of anal fin beneath end of dorsal fin or slightly behind last dorsal ray. Ventral bases in advance of dorsal origin. No adipose fin. ORB 1, below front

margin of eye. OP 3, upper one about level with center of eye, lower two level with end of maxillary. Additional photophores present on head above maxillary, in a row along posterior portion of lower jaw (the first of these larger), and lower surface of symphysis of lower jaw (2-4 minute, round spots, perhaps photophores). SO present, somewhat behind symphysis, hidden by lower jaw. BR 8-16. Body with ventral and lateral rows of photophores typical of family and also several rows above these; photophores present on isthmus. IV 30-49. VAV 12-17. AC 28-49, straight. IC 70-113. OA 45-87. Always a third row of photophores along lateral line from upper edge of gill opening to caudal fin, 65-98 organs, last one or two on caudal fin. Older specimens with additional serial rows of photophores above and below lateral line, and 1-3 photophores on or before pectoral base between ventral and lateral series. A pair of narrow strips of pale tissue, probably luminous, on ventral surface of body below eighth to seventeenth IV photophores. Fin rays: dorsal 9-13, anal 36-68, pectoral 8-11, ventral 7-8. Branchiostegal rays 11-14 (15-16?), bases prominent but without spines. Vertebrae 63 to *ca.* 85, or more.

Remarks. Diplophos is probably related to both *Yarrella* and *Gonostoma.* Its affinities with the former are set forth in the key to the genera on page 70, and in addition these two genera have a relatively long premaxillary. The relationship of *Diplophos* to *Gonostoma* is less obvious, but their common origin is possibly indicated by the similarity of their dentition and of their photophore structure (Brauer, 1908, p. 18), as well as in their tendency toward the development of luminous tissue on head and body. *Diplophos* may also be distantly related to the maurolicid group of genera (see p. 61).

Manducus Goode and Bean 1895 is reduced to the rank of subgenus because the distinction between this genus and *Diplophos* is of noticeably different value than distinctions between other gonostomatid genera and the differences appear to be of a specific rather than a generic nature, as shown in the key on page 70. However, *Diplophos, sensu stricto,* probably contains two or more closely related species that differ rather sharply from *maderensis,* the only known species of *Manducus,* and the latter name is therefore retained as a subgenus of *Diplophos.*

Subgenus DIPLOPHOS Günther 1873

In the following characters the subgenus *Diplophos* differs from the subgenus *Manducus* (cf. p. 81).

Angle of preopercle nearly vertical or slightly rounded. Pseudobranchiae sometimes present. Gill rakers 7-9 + 3 on first arch. Premaxillary about the same length as, or slightly shorter than, toothed portion of maxillary. Head and trunk about the same length as tail or slightly shorter. Origin of dorsal fin about in middle of body length but as far as known always slightly nearer tip of snout than caudal base. Origin of anal fin beneath end of dorsal fin or just behind its last ray. Ventral bases noticeably in front of dorsal origin. Photophores on upper part of head, in addition to the ORB and OP, consisting of one, level with ORB, on cheek above middle of maxillary; a row of 9-13 minute organs on cheek below eye, hidden beneath subocular bone; 2-4 small organs beneath posterior end of maxillary; small photophores also sometimes present on opercle above lower posterior OP and between the two lower OP. Area just below symphysis of lower jaw with two small round spots (photophores?) on each side. A row of 12-16 minute photophores on posterior portion of lower jaw, the first one enlarged. Patches of luminous tissue sometimes present on opercle, maxillary and tongue. BR 10-12 + 0-3. IV 40-49. VAV 13-17. AC 43-49, last two or three usually, but not always, slightly separated from the rest. IC 97-113. OA 66-87, sometimes ending above middle of anal fin, sometimes reaching caudal base. Lateral line row (80?) 86-98. A pair of narrow strips of pale tissue, probably luminous, below ninth to seventeenth IV photophores. Anal rays (43?) 53-68. Vertebrae *ca.* 85 (one eastern Pacific specimen).

It is impossible to determine the number of species contained in the *D. taenia* complex without examining a large series of specimens from different areas. Variation in fin ray and photophore counts is rather wide but specimens are too rare to determine the significance of these variations. The photophores of the ventral series are consistently fewer in Pacific specimens. Atlantic specimens are all in pretty good agreement with one another but even here there is enough variation, especially in the number of anal rays, to allow the possibility at least of subspecific differences. All Atlantic specimens are considered here

to belong to a single species, *D. taenia* Günther. The small specimen reported by Brauer (1906, p. 89) from the Indian Ocean agrees with Atlantic specimens. Norman (1939, p. 19) also reported, as *taenia,* two small specimens from the Indian Ocean. They were not described.

Brauer (1906, p. 90) described the BR as follows: "15-16 between the branchiostegal rays, the twelfth smaller and the last three smaller and separated by a large interspace from the others and from one another." No trace of these smaller organs has been found on Atlantic specimens examined but one to three are present on several eastern Pacific specimens. The description quoted suggests that the first 11-12 BR are analagous with the 11-12 of most of the specimens examined.

Diplophos taenia Günther 1873
Atlantic specimens

In the Atlantic, *D. taenia* has been reported from various localities between about 40° N. and 30° S.; and in the Indian Ocean off Natal, between the Seychelles and Zanzibar, and in the Arabian Sea. Counts and proportions of some Atlantic specimens are shown in Table 1. Included are two hitherto unreported specimens, U.S.N.M. Nos. 100525 and 100616, caught in 1914, at *Grampus* (*Bache*) Station 10182, off Bermuda, 30° 27′ N., 66° 05′ W., 19 February, surface; and Station 10196, northeast Providence Channel, Bahamas, 25° 27′ N., 77° 16′ W., 3 March, surface.

Both of these specimens are small, their standard lengths being 74 and 66 mm. No pseudobranchiae are visible. There are a few minute teeth on each side of the vomer in the larger specimen but none can be seen in the smaller one. Both have a single row of 6-9 small teeth on each palatine and there are no teeth on either the pterygoids or the tongue. A pair of thread-like strips of luminous(?) tissue is present on the ventral surface of the body below the fourteenth to seventeenth IV photophores. The OA number 71 and 73 and extend to a vertical from the middle of the anal fin; the organs decrease in size posteriorly. In addition to the IC, OA, and lateral line photophores, the following rows are present: between the IC and OA *one* row of minute dots reaching well past the anal origin in the larger

specimen, not quite reaching the ventral base in the smaller; between the OA and lateral line *one* row of minute dots extending about to the anal origin in the larger fish and halfway between the ventrals and the anal origin in the smaller one; above the lateral line *three* similar rows in the larger specimen, only *one* in the smaller one, reaching below or beyond the dorsal fin.

Pacific specimens

The following ten specimens of the *taenia* complex have been reported from the Pacific Ocean, most of them caught at the surface.

The type of *Diplophos pacificus* Günther 1889, length 37 mm., 5° 24′ N., 147° 02′ W., found in a townet attached to the dredge after a deep haul; inadequately described and now in poor condition.

The type of *Diplophos proximus* Parr 1931, standard length *ca.* 82 mm., Gulf of California, 24° 07′ N., 108° 40′ W., 523 meters; differs from *taenia* in number of photophores but not significantly in proportions.

A specimen 43 mm. long from the Solomon Islands, identified as *D. pacificus* but not described, by Seale (1935, p. 340).

The type of *Diplophos taenia orientalis* Matsubara 1940, total length 195 mm., standard length 179.8 mm., off Huji River, near Kambara, Japan, 306 meters; largest known specimen of the group, differing from *taenia* principally in photophore counts.

A second specimen of *D. orientalis*, total length *ca.* 195 mm., taken off Kambara, Suruga Bay, Japan (Abe, 1958, p. 1241, pl. 238, fig. 598).

Five specimens, 34-41 mm. long, Sulu Sea, 6° 48.5′ N., 118° 51.5′ E., surface at night, identified as *D. taenia* and partially described by Herre and Herald (1950, p. 314, fig. 2).

Twelve hitherto unreported Pacific specimens from the collection of Scripps Institution of Oceanography have been examined:

Western Pacific: One, standard length 40 mm., SIO 56-127, Marshall Island area, 13° 03′ N., 166° 04′ E., to 13° 03′ N., 166° 32′ E., 0-400 fathoms (0-732 meters).

Eastern Pacific: Five, standard length 42 and 89-100 mm., SIO 54-89, off the Revillagigedo Islands, 19° 09′ N., 110° 58.5′ W., 0-825 fathoms (0-1509 meters); one, standard length 100.5 mm.,

SIO 54-93, same area, 21° 01′ N., 115° 39′ W. to 21° 04.5′ N., 115° 48′ W.; one, standard length 90 mm., SIO 54-88, same area, 20° 16′ N., 111° 32.2′ W. to 20° 03.2′ N., 111° 20′ W., 0-25 fathoms (0-45 meters); two, standard length 81 and 88.5 mm. SIO 54-92, same area, 19° 52′ N., 113° 20.5′ W., to 19° 57.5′ N., 113° 32.5′W., 0-100 fathoms (0-183 meters); one, standard length 91 mm., SIO 55-213, west of Clipperton Island, 11° 13′ N., 120° 57′ W., 0-63 fathoms (0-115 meters); one, standard length 97.5 mm., SIO 54-95, off Lower California, 23° 05′ N., 119° 08′ W. to 22° 23′ N., 119° 36′ W., 0-1333 fathoms (0-2438 meters).

Counts and proportions of some of these Pacific specimens are shown in Table 2, those of Atlantic specimens in Table 1. The consistently lower counts found in Pacific specimens suggest that they belong to a distinct species or subspecies. It is unfortunate that the type of *D. pacificus*, the first species described from the Pacific, is small and now in poor condition, and it is also unfortunate that no large Atlantic specimens are available for comparison with eastern Pacific specimens. Small but well developed pseudobranchiae are present on all of the larger eastern Pacific specimens and their apparent absence in Atlantic specimens examined is probably questionable, especially as Brauer (*loc. cit.*) noted their presence in an eastern Atlantic example.

The eastern Pacific specimens have one small tooth on each side of the vomer; and a row of four to seven small teeth and some additional minute teeth on each palatine. There are no teeth on the pterygoids, and usually none on the tongue, but several specimens do have a cluster of three or four very small teeth at the tip of the tongue. Small teeth on the tip of the tongue were described in both specimens of *D. orientalis* but have not been mentioned in any other description of a *Diplophos* except *maderensis*. Larger specimens have three tiny photophores in a vertical series above the lower posterior OP, and several in a horizontal series between the two lower OP. All eastern Pacific specimens except the smallest have a pair of thread-like strips of luminous(?) tissue below the ninth to fifteenth IV photophores (below the fourteenth to seventeenth in the two Atlantic specimens examined). The OA number 60-61 and reach a vertical from about the middle of the anal fin in three specimens. On a fourth they number 84 and reach the

caudal base, but the organs on the latter half of the tail are minute. Few of these Pacific fishes are intact but those retaining most of their skin possess the following rows of minute photophores on the body: between the IC and OA *one* row, reaching slightly past the anal origin; between the OA and lateral line *three* rows, the lower and upper reaching well past the anal origin and the middle row to about halfway between the ventral bases and the anal origin; above the lateral line *three* rows, one of them reaching the caudal base.

The 40 mm. specimen taken off the Marshall Islands lacks both pterygoid and tongue teeth, and has no luminous tissue on the ventral surface of the body; the premaxillary and toothed portion of the maxillary are equal in length; two small teeth are present on each side of the vomer; and each palatine bears five small teeth.

D. orientalis Matsubara should probably be retained as a distinct species, at least until intermediate sizes are found. In appearance it somewhat resembles *D. maderensis*, although its characters are distinctly those of the subgenus *Diplophos*. A similarity to *Manducus* is seen in the deeper body and the heavy, fang-like premaxillary teeth. Even in the largest eastern Pacific specimen seen, standard length 100.5 mm., the long premaxillary teeth are slender and needle-like. It is possible, of course, that *D. orientalis* merely represents the adult Pacific *Diplophos*. The higher OA count (87), greater body depth, and even the enlarged premaxillary teeth, might be attributed to the large size of the only two specimens known (177 and *ca.* 180 mm. in standard length). On the other hand, one of the eastern Pacific specimens (SIO 54-88), 90 mm. in standard length, is a female with large ovaries which contain small and probably immature eggs. It is interesting that Abe (1958, p. 1242) described a narrow, semi-transparent band along the mid-ventral line of this species, with the inference that the area may be luminous.

Subgenus MANDUCUS Goode and Bean 1895

The subgenus *Manducus* differs from the subgenus *Diplophos* in the following respects (cf. p. 77).

Angle of preopercle slightly acute. No pseudobranchiae. Gill rakers 8-9 + 3-5 on first arch. Premaxillary at least as long as

toothed portion of maxillary, sometimes slightly longer. Head and trunk longer than tail, proportionately more so in adult. Origin of dorsal fin slightly behind middle of body length, close to mid-body in young. Origin of anal fin slightly behind a vertical from last dorsal ray. Ventral bases slightly in front of dorsal origin. Photophores all relatively inconspicuous, some on head (especially the SO and lower anterior OP) obscured by bone. On upper part of head in addition to ORB and OP, one small organ above anterior toothed portion of maxillary; a second one level with and not far behind it; and one small photophore beneath end of maxillary. Area just below symphysis of lower jaw blackish and occupied by two short series of 2-4 minute ring-like spots (photophores?). A row of about 10-13 minute photophores on posterior portion of lower jaw, the first one enlarged. No patches of luminous tissue on head or body as far as known except a pair of narrow strips of pale tissue, possibly luminous, below eighth to eleventh or twelfth IV photophores. AC photophores evenly spaced. BR 8-9. IV 30-33. VAV 12-14. AC 28-30. IC 70-75. OA 45-48, reaching about to or beyond middle of anal fin and followed by 12-17 much smaller organs, which reach caudal base in complete specimens. Lateral line row 65-68. Anal rays 36-41. Vertebrae 63.

The subgenus contains only the following species.

Diplophos maderensis (Johnson) 1890

This species is known only in the North Atlantic, and the only adults recorded in the literature have been found at Madeira. It is therefore of interest that during a recent cruise made by the *Oregon* twenty specimens, 94.5-144.5 mm. in standard length, were caught in a trawl off Surinam at Station 2008, 7° 38′ N., 54° 43′ W., 7 November 1957, in 250 fathoms (457 meters). I have also examined five specimens, 98.5-133 mm. in standard length, sent by Mr. G. E. Maul from Madeira, where they were found on the beach at Funchal in November 1954; and one young specimen, standard length 32 mm., from the Bahamas, reported under the name *Diplophos minutus* by Parr (1937, p. 46).

The following counts have been made on adult specimens: dorsal rays 12-13, anal rays 38-41, pectoral rays 10-11, ventral rays 8, branchiostegal rays 11-3, gill rakers on first arch 8-9 + 3-5,

vertebrae 63 (counted on an X-ray photograph of one Madeiran specimen). BR 8-9; IV 30-33, the last one or two smaller and situated just in front of or on ventral bases; VAV 12-13; AC 28-30; IC 70-75; OA 45-48, followed by smaller organs to caudal base; lateral line *ca.* 65-68.

Each premaxillary has a row of 3-7 enlarged teeth of varying sizes, the second and third the largest, and a few very small teeth between the fangs; all of these teeth are inclined slightly backward. On the maxillary is a row of closer-set, unequal teeth, all straight and all smaller than the long premaxillary teeth. On each mandible is a row of widely spaced fangs and posteriorly a few smaller teeth between the fangs. Anteriorly, there are no small teeth between the fangs but there is an outer row of 4-6 teeth, smaller than the fangs but larger than the interspace teeth.

There are 1-6 small teeth on each side of the vomer; a row of 9-15 small teeth on each palatine, the first one or two slightly enlarged; a patch of minute teeth on each pterygoid; and a cluster of small teeth near the tip of the tongue. It should be noted that Maul (1948, p. 33) found no vomerine teeth on three specimens from Madeira although these are present in all specimens examined, including six from Madeira; and that Welsh (1923, p. 1) found no palatine teeth on juvenile specimens from the Bahamas and Florida. Welsh also reported eleven BR photophores, while specimens examined have only eight or nine, and a higher number has not been mentioned by other authors. It is possible that the two lower opercular organs were included in Welsh's count.

The scales are mostly lost but it is evident that the dorsal and ventral surfaces are fully scaled, neither "rugosely warted" as described by Johnson (1890, p. 458), nor "keeled" as described by Maul (*loc. cit.*).

In addition to the IC, OA and lateral line rows, the following rows of photophores are present on the body: between the OA and the lateral line, *three* rows of smaller organs, the first of these reaching about to a vertical from the middle of the anal fin and continued posteriorly as still smaller round spots, sometimes to the end of the anal fin, sometimes to the base of the caudal; the second is traceable in one specimen nearly to the end

of the anal but is shorter in other specimens; and the third is obscure, apparently shorter, not reaching the anal origin. Above the lateral line are *two* rows of obscure spots, reaching at least beyond the end of the dorsal fin, sometimes to a vertical from the middle of the anal fin; and, in two specimens, a *third* row commencing in one instance above the other two, in the other case beneath the anterior portion of the dorsal fin. There is also *one* row of small round organs between the IC and OA, reaching to beneath the last of the larger OA organs.

The following measurements, in per cent of the standard length, are based on six western Atlantic specimens, standard length 94.5-144 mm., and five specimens from Madeira, standard length 98.5-133 mm. The figures in parentheses refer to the latter. Depth 15.8-16.9 (15.5-16.8); head 20.1-21.3 (21.1-21..6); snout 4.4-5.1 (4.5-5.1); orbit 3.6-4.2 (3.3-3.8); interorbital width at center of eye 3.7-4.1 (4.0-5.1); upper jaw 14.6-15.5 (14.8-15.6); premaxillary 7.4-7.9 (7.5-7.9); toothed portion of maxillary 6.9-7.8 (7.2-7.8); tip of snout to dorsal origin 51.8-53.1 (49.5-52.2), to anal origin 61.5-62.5 (59.0-63.0), to ventral bases 45.5-46.8 (45.2-46.3); distance between first anal ray and base of middle caudal rays 36.5-39.2 (37.6-41.2), last anal ray and base of middle caudal rays 5.9-7.6 (6.0-7.2), last dorsal ray and base of middle caudal rays 38.1-40.2 (38.7-40.0), ventral bases and anal origin 14.7-16.9 (14.8-17.6); least depth of caudal peduncle 5.4-5.9 (4.3-5.1); dorsal base 7.2-8.7 (8.0-8.7); anal base 30.3-31.8 (30.0-34.0); pectoral length *ca.* 16.2 (one specimen only); ventral length 9.75-11.1 (all broken in Madeiran specimens).

Yarrella Goode and Bean 1895

Yarrella Goode and Bean, 1895, Ocean. Ichth., p. 103, type species *Yarrella blackfordi* Goode and Bean 1895, Gulf of Mexico, 324 fathoms (593 meters); Jordan and Evermann, 1896, Bull. U. S. Nat. Mus., **47:** 583.

Lychnopoles Garman, 1899, Mem. Mus. Comp. Zool., **24:** 244.

Diplophos Parr, 1931, Bull. Bingham Oceanogr. Coll., **2** (4): 11 (part, *Lychnopoles* in synonymy).

Manducus Fowler, 1936, Bull. Amer. Mus. Nat. Hist., **70:** 1202 (part, *Lychnopoles* in synonymy).

Generic characters. Eye normal, moderate. Snout longer than orbit. Interorbital width at center of eye greater than diameter of orbit. Mouth large, oblique; edge of premaxillary straight

laterally; toothed edge of maxillary slightly convex, nearly reaching preopercle. Premaxillary longer than toothed portion of maxillary. Angle of preopercle quite acute. Teeth of upper jaw biserial on premaxillary, those of inner row smaller and curving inward; uniserial on maxillary. Teeth of lower jaw biserial, similar to those of premaxillary but somewhat smaller. Vomer with one to three small teeth on each side. Palatines each with a short row of two to six small teeth. Pterygoids usually toothless but a few specimens seen with one or several microscopic teeth present. Tongue toothless. Gill rakers 12-16 + 6-7 = 18-22 on first arch. Spines on inner edge of first gill arch very short, a row of minute spines below each one. No pseudobranchiae. Scales present, very deciduous. Anus close to anal fin. Head and trunk longer than tail. Dorsal origin about in middle of body length or slightly behind it. Anal origin beneath middle or front of dorsal fin. Ventral bases well ahead of doral origin. No adipose fin. ORB 1, in front of lower margin of eye. OP 3, obscure, upper one level with upper edge of pupil, lower ones level with end of maxillary. SO present, slightly behind symphysis and somewhat laterally situated. BR 11-13. Body with ventral and lateral rows of photophores typical of family and also several rows above these. Photophores present on isthmus. IV 9 + 3-4 + 11-12 = 23-25. VAV 9-12. AC 20-28, straight, 6-10 of them behind anal fin. IC 52-64. OA probably always about 50 or more, reaching caudal base. No additional photophores on head, and no patches of luminous tissue on head or body as far as known. Fin rays: dorsal 14-16 (17 in one specimen of *blackfordi*), anal 28-31, pectoral 8-10, ventral 6-7. Branchiostegal rays 13-16, no spines at bases. Vertebrae 45-54.

Remarks. Yarrella shows relationship to *Triplophos* in the arrangement of the body photophores, the long premaxillary, and the dentition; and to *Polymetme* in dentition, the position of the fins, and many proportions. An examination of two specimens from the type lot of *Lychnopoles argenteolus* Garman has shown them to be congeneric with *Y. blackfordi*. As in the latter, the toothed portion of the maxillary is slightly shorter than the premaxillary, the dentition is similar (although the teeth of *Y. argenteola* are somewhat smaller than those of *Y. blackfordi*), and the pattern and arrangement of the body photophores are

similar in the two species. Specific differences are set forth in Table 3.

The discovery that *Yarrella* has more than two rows of photophores on the body clarifies the confusion that has resulted in the past from a misunderstanding of the genus, and necessitates the removal of all species described under the name except the type species, *blackfordi*. Although the species referred here to *Polymetme* do appear to be somewhat related to *Yarrella*, the rather common, small form, *Pollichthys mauli* (Poll), confused with *Y. blackfordi* until renamed *Y. mauli* by Poll (1953, p. 59), is quite different and, as noted by Jespersen and Tåning (1919, p. 223), is more closely related to *Vinciguerria*.

Yarrella blackfordi Goode and Bean 1895
Figure 2

Yarrella blackfordi Goode and Bean, 1895, Ocean. Ichth., p. 103, fig. 121; Jordan and Evermann, 1896, Bull. U. S. Nat. Mus., **47:** 584; 1900, *op. cit.*, fig. 249; Poll, 1953, Rés. Sci. Exp. Océanogr. Belge (1948-1949), **4** (2), (3): 56, fig. 22; Springer and Bullis, 1956, Spec. Sci. Rep. U. S. Dept. Int., Fish., **196:** 50 (part).

The following unrecorded specimens have been examined.

Gulf of Mexico, *Oregon:* Station 126, 29° 02′ N., 88° 34.5′ W., 23 September 1950, 195 fathoms (357 meters); one specimen, standard length *ca.* 202 mm. Station 279, 29° 11′ N., 86° 52′ W., 24 February 1951, 305 fathoms (558 meters); three specimens, 180-200 mm. Station 543, 27° 38.2′ N., 94° 59.4′ W., 16 April 1952, 350-400 fathoms (640-732 meters); two specimens, 170 and 261 mm. Station 597, 29° 13′ N., 87° 59′ W., 10 July 1952, 280 fathoms (512 meters); two specimens, 212 mm. Station 640, 20° 01′ N., 88° 24′ W., 19 September 1952, 355-475 fathoms (649-869 meters); two specimens, 200 and 212 mm. Station 1019, 24° 16′ N., 83° 22′ W., 16 April 1954, 375 fathoms (686 meters): one specimen, 200 mm. Station 1272, 28° 20′ N., 89° 46′ W., 8 March 1955, 250 fathoms (457 meters), 49°F. at bottom; two specimens, U.S.N.M. No. 157908, 204 and 213.5 mm.

Off northern South America, *Oregon:* Station 1980, 10° 10′ N., 59° 54′ W., 3 November 1957, 350 fathoms (640 meters), 58.6°F. at bottom; one specimen, 163 mm. Station 2009, 07° 40′ N., 54°

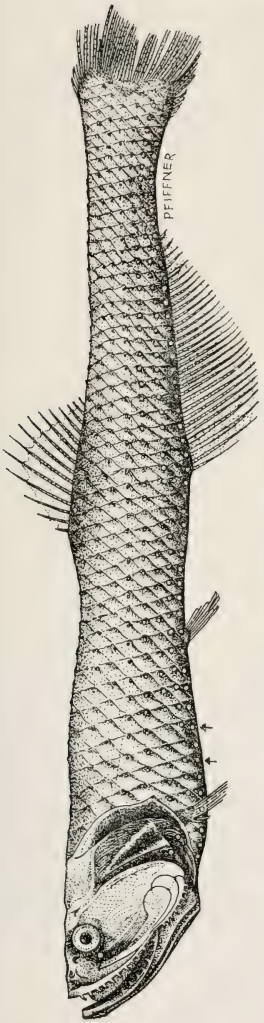

Figure 2. *Yarrella blackfordi* Goode and Bean. *Oregon* Station No. 2010, Standard length 193 mm.

Figure 2a. Vertical section, enlarged, of area indicated by arrows.

47′ W., 7 November 1957, 300 fathoms (549 meters); five specimens, 190-200 mm. Station 2010, 07° 44′ N., 54° 40′ W., 7 November 1957, 350 fathoms (640 meters); fifty-four specimens, 133-222 mm. Station 2011, 07° 46′ N., 54° 36′ W., 7 November 1957, 400 fathoms (732 meters); eight specimens, 144.5-274 mm.

One specimen, 222 mm., Stanford University No. 9486, *Albatross* Station 2376 (type locality), 29° 03′ 15″ N., 88° 16′ W., Gulf of Mexico, 324 fathoms (592 meters).

One specimen, 148.5 mm., University of Miami Marine Laboratory No. 1678, *Antilles,* Gulf of Mexico, 28° 36′ N., 89° 49′ W., 234 fathoms (428 meters).

The only certain previous records of *Y. blackfordi* are the type series (three specimens) from the Gulf of Mexico and thirty-nine specimens reported by Poll (1953, p. 56) from the eastern Atlantic off Africa, 5°-11° S. The two larger specimens mentioned by Longley and Hildebrand (1941, p. 15), taken south of Tortugas in 672-686 meters, may have been *blackfordi,* but the smaller one, which I have examined, belongs to *Polymetme corythaeola.* Other Atlantic reports were of undescribed material and either cannot be identified or are referable to *Pollichthys mauli.* Two little specimens tentatively identified as *Y. blackfordi* by Koefoed (1958, p. 6) have been examined and are not referable to this species. The larger one is a young *Gonostoma,* sp. indet., and the smaller, which is in very poor condition, appears to be a juvenile maurolicid but cannot be identified further.

The skin of this species is extremely fragile and is almost entirely lost in most of the specimens at hand. In fact, not a single specimen has its full complement of skin, although many from *Oregon* Station 2010 retain much of it. Many of the photophores, especially those of the lateral and accessory series, have been lost with the skin and the condition of other recorded specimens was apparently similar. Dr. Leonard P. Schultz has been kind enough to examine the types of *Y. blackfordi* and has written (*in litt.,* 1956) that these still retain shreds of skin on which are found portions of the rows of photophores above the lateral series.

The photophores are moderate to small in size and are rather inconspicuous. There are usually 12 BR (13 in one specimen)

and other counts are as follows: IV 9 + 3-4 + 11-12 = 24-25, the three or four pre-pectoral organs smaller than those preceding or following them; VAV 12; AC 24-27 (28 in one specimen), eight to ten of them behind anal fin; OA probably always reaching caudal base, count indeterminable on all but three specimens, on which were counted 52, 52 and 53 photophores. Above the OA are *three* rows of photophores, the *first* of these (just above the OA), apparently reaching a little beyond the ventral bases and numbering about 15-16 organs. The *second* and *third* rows reach the caudal base but the number of photophores, which are very small posteriorly, is indeterminable. In addition to the photophores described there are clusters of minute round organs on the edges of the scale pockets. These are associated with all serial photophores above the ventral row (IC) and also form *two* rows above the uppermost row of serial photophores, both rows of clustered organs reaching the caudal base.

Triplophos Brauer 1902

Triplophos Brauer, 1902, Zool. Anz., **25:** 282; type species *Triplophos elongatus* Brauer 1902 = *Photichthys hemingi* McArdle 1901; 1906, Wiss. Ergebn. Deutschen Tiefsee Exp. Valdivia, **15** (1): 98; Norman, 1930, Discovery Rep., **2:** 296; Misra, 1953, Rec. Indian Mus., **50:** 398.

Generic characters. Eye normal, moderate. Snout shorter than orbit. Interorbital width at center of eye equal to diameter of orbit or a little shorter. Mouth large, slightly oblique; edge of premaxillary straight, toothed edge of maxillary slightly convex, nearly reaching preopercle. Premaxillary much longer than toothed portion of maxillary, which is very short and scarcely enters the gape. Angle of preopercle very acute. Premaxillary teeth biserial, well spaced, those of inner row curving inward (described as uniserial by Brauer). Maxillary with only a few teeth in a single row. Teeth of lower jaw in specimens examined similar to those of premaxillary, outer row set slightly lower and curving inward; described as uniserial by other authors. Vomer toothless or with one tooth on each side. Palatines each with a short row of small teeth, the anterior one sometimes slightly enlarged. Pterygoids with or without teeth. Tongue toothless. Gill rakers 14-16 + 9 = 23-25 on first arch. Spines on inner edge of first gill arch short, a row of minute prickles below each one.

No pseudobranchiae. Scales present but very deciduous. Anus close to anal fin. Head and trunk much shorter than tail. Dorsal origin far in advance of middle of body length. Anal origin beneath last dorsal ray or just behind a vertical from it. Ventral bases a little in front of dorsal origin. No adipose fin. ORB 1, below center of eye. OP 3 (more easily seen from inside opercle), upper one level with upper margin of eye, lower anterior one beneath maxillary, lower posterior one on same level. SO present, slightly behind symphysis, hidden by lower jaw. BR 8-13. Additional photophores on head: one, large, above maxillary; and a row of tiny organs above and close to premaxillary. Body with ventral and lateral rows of photophores typical of family and also several rows or partial rows above these. Photophores present on isthmus. IV 24-30, one or two raised toward pectoral base, those following commencing below the last retinal organ. VAV 5-7. AC 35-41, straight, two or three of them behind anal fin. IC 68-76. OA 50-56, the first 9-11 lower than those following. Above OA three or four additional rows of photophores. No patches of luminous tissue on head or body as far as known. Fin rays: dorsal 10-12, anal 54-63, pectoral 9-11, ventral 6-7. Branchiostegal rays 11-14 (17?), no spines at bases. Vertebrae probably *ca.* 60 (counted from X-ray photograph of one specimen, indistinct on tail).

Remarks. *Triplophos* stands apart from all other gonostomatid genera in the relative lengths of the premaxillary and maxillary bones, and from all except *Danaphos* in the advanced position of the dorsal fin. It is perhaps most closely related to *Yarrella*. According to Brauer (1908, pp. 27, 123) *Triplophos* is similar to *Diplophos* in some ways, but the structure of the photophores is close to that of *Maurolicus* and *Valenciennellus*, as well as the Sternoptychidae. The fact that the premaxillary forms almost the entire upper jaw somewhat strengthens the relationship between *Triplophos* and *Yarrella*, the latter having a lengthened premaxillary as well as additional photophores on the body. Brauer's statement (1906, p. 99) that the premaxillary is short in *Triplophos* must have been an error. In specimens at hand it forms almost the entire upper border of the mouth, the maxillary being reduced to a small round knob bearing five or six small teeth.

The generic diagnosis has been based in part on previous descriptions of specimens from the eastern Atlantic and the Indian Ocean, and in part on the newly discovered western Atlantic specimens listed below.

Triplophos hemingi (McArdle) 1901

Photichthys hemingi McArdle, 1901, Ann. Mag. Nat. Hist., (7) **8:** 521; Alcock and McGilchrist, 1905, Ill. Zool. Investigator, Fishes, pl. 36, fig. 2 (holotype).

Triplophos elongatus Brauer, 1902, Zool. Anz., **25:** 282; 1906, Wiss. Ergebn. Deutschen Tiefsee Exp. Valdivia, **15** (1): 99, pl. 7, fig. 4, text fig. 41 (*elongatum*); 1908, *op. cit.*, **15** (2): 27, 176, pl. 22, figs. 4-7, pl. 36, fig. 8 (*elongatum*); Misra, 1950, Rec. Indian Mus., **45:** 415 (*elongata*); 1953, *op. cit.*, **50:** 399, fig. 15b.

Triplophos hemingi Lloyd, 1909, Mem. Indian Mus., **2:** 150; Norman, 1930, Discovery Rep., **2:** 296; Poll, 1953, Rés. Sci. Exp. Océanogr. Belge (1948-1949), **4.** (2), (3): 61, fig. 25.

Three specimens, 106-130 mm. in standard length, *Oregon* Station 1907, Caribbean Sea off Central America, 12° 25′ N., 82° 23′ W., 11 September 1957, trawl, 400-425 fathoms (732-778 meters); one specimen, 122 mm., *Oregon* Station 1916, same area, 13° 18′ N., 82° 12′ W., 12 September 1957, trawl, 350 fathoms (640 meters); two specimens, *ca.* 176 mm., *Oregon* Station 2007, off Surinam, 07° 34′ N., 54° 49′ W., 7 November 1957, trawl, 225 fathoms (411 meters), 47.5°F. at bottom.

Although these specimens differ slightly from descriptions based on Indian Ocean specimens, the differences do not seem important enough to warrant their separation as a distinct species. All six specimens examined have seven VAV photophores, in contrast to a count of five in Indian Ocean examples. However, Brauer's figure (1906, p. 99, fig. 41) shows six photophores between the ventral bases and the anal origin; and Poll (1957, *in litt.*) has written that VAV counts in sixteen of the eastern Atlantic specimens reported by him in 1953 are seven, six, and (in one specimen) five. The IV count of our specimens is lower, 24-25 (29-30 in Indian Ocean specimens). The first row of serial photophores above the OA has been described and figured as short, and the one above it with a count of 36-43. In specimens examined this short row appears to be continuous

with the row that extends on the tail, but the first nine photophores are on a lower level than those following. Similarly, the first nine organs of the OA series are slightly below those following them. The uppermost rows of photophores are smaller and do not reach the tail.

The only significant proportional differences noted (Table 4), a shorter pre-anal distance and a longer anal base in Indian Ocean specimens, need to be verified by direct comparison of material from both oceans. Further information is also needed on the jaw teeth. The teeth on the premaxillary have been described as biserial, as they are in specimens examined, by all authors except Brauer. However, all authors have stated that the lower jaw teeth are in a single row, and in the western Atlantic specimens there is, along most of the mandible, an outer row of teeth, curving inward and set somewhat below the inner row.

The vomer is toothless or has one minute tooth on each side. Each palatine has a short row of 2-6 teeth, microscopic in size excepting the first one or two. The pterygoids and tongue are toothless.

The photophores are moderate in size. The row of tiny organs above the premaxillary is usually difficult to see, or damaged. The OA organs number 50-55, the first nine slightly lower than those following, and those on the tail diminishing in size posteriorly. These reach the end of the anal fin in one specimen (*ca.* 118 mm. in standard length), not quite to the end of the anal fin in others. Above the OA are three or four rows of small photophores, 39-47 in the lowest of these, which reaches beyond the middle of the anal fin in all but the smallest specimen; the first nine are on a slightly lower level. The upper rows of photophores are not complete. An additional photophore is present close to the opercle between the IC and the OA.

Polymetme McCulloch 1926

Polymetme McCulloch, 1926, Biol. Res. Endeavour, **5:** 166; type species *Polymetme illustris* McCulloch 1926, southern Australia; Barnard, 1927, Ann. So. Afr. Mus., **21:** 1018; McCulloch, 1929-30, Mem. Australian Mus., **5:** 51.

Yarrella Barnard, 1925, Ann. So. Afr. Mus., **21:** 148; Norman, 1930, Discovery Rep., **2:** 288 (part); Matsubara, 1938, Jour. Imp. Fish. Inst. Tokyo, **33:** 44 (part); Smith, 1949, Sea Fishes So. Afr., p. 104 (part); Misra, 1953, Rec. Indian Mus., **50:** 398.

Generic characters. Eye normal, moderate. Snout about equal to diameter of orbit. Interorbital width at center of eye about equal to or a little less than diameter of orbit. Mouth large, oblique, edge of premaxillary straight; toothed edge of maxillary slightly convex, nearly reaching preopercle. Premaxillary more than half as long as toothed portion of maxillary. Angle of preopercle acute. Teeth of upper jaw biserial on premaxillary, uniserial on maxillary. Teeth of lower jaw biserial, those of outer row larger. Vomer with one to three teeth on each side. Palatines each with a short row of small teeth. Pterygoids with a rather large patch of minute teeth (not described in type species, *illustris*). Tongue toothless. Gill rakers 9-12 + 5-8 = 15-19 on first arch. Spines on inner edge of first gill arch very short, a cluster of minute prickles below each one. No pseudobranchiae. Scales present but very deciduous. Anus close to anal fin. Head and trunk a little longer than tail. Dorsal origin about in middle of body length. Anal origin beneath end of dorsal fin or just behind a vertical from its last ray. Ventral bases noticeably ahead of dorsal origin. Adipose fin above end of anal fin. ORB 1, in front of lower margin of eye. OP 3, upper one smaller, about on a level with upper border of pupil or higher; lower anterior one just behind maxillary; lower posterior one slightly higher. SO present. BR 9-10. No other photophores on head. Body with two rows of photophores; photophores present on isthmus. IV 19-21, ninth or tenth raised toward pectoral base. VAV 7-8. AC 21-25, first one or two elevated and sometimes elongate, five to eight of them behind anal fin. IC 50-54. OA 16-18, not always perfectly straight, ending above next to last VAV. No additional photophores and no patches of luminous tissue on head or body as far as known (but see p. 99). Fin rays: dorsal 11-13, anal 24-33, pectoral 9-11, ventral 7 (8?). Branchiostegal rays 12-14, no spines at bases. Vertebrae 45, counted from an X-ray photograph of one western Atlantic specimen.

Remarks. Polymetme is apparently related to *Yarrella,* judging by the relatively long premaxillary and the partially biserial teeth on the jaws. It differs, however, in the number and arrangement of the serial rows of photophores, in the larger and more conspicuous individual photophores, and in having an adipose fin.

Polymetme is similar to *Pollichthys* in the possession of an adi pose fin, the length of the anal fin, the number of BR photophores, and in having only two rows of body photophores. It differs from that genus principally in having only one ORB, ten pectoral rays (eight in *Pollichthys*) and two rows of teeth on the premaxillary.

This genus has for many years been considered synonymous with *Yarrella* and is reinstated here to include the following species, some or most of which are probably synonymous: *Diplophos corythaeolum* Alcock, Andaman Sea (and *Yarrella corythaeola* Poll, West Africa); *Yarrella africana* Gilchrist and von Bonde, Natal coast; *Polymetme illustris* McCulloch, Australia (and *Yarrella blackfordi illustris* Matsubara, Japan); *Yarrella blackfordi elongata* Matsubara, Japan; and *Yarrella surugaensis* Matsubara, Japan. In the absence of comparative material it is not possible to determine the number of valid species belonging to the genus, but *africana* is probably a synonym of *corythaeola*. *surugaensis* is probably the same as *illustris*, and actually all four of these species may be synonymous. *P. surugaensis* was distinguished from *P. illustris* on the basis of the irregularity of the OA photophores and slight differences in the number of anal rays, gill rakers, and AC photophores. These small variations do not seem to warrant the separation of *surugaensis*, particularly in view of the fact that the OA photophores are usually irregular in specimens examined from the western Atlantic.

In the original diagnosis of the genus, McCulloch (1926, p. 166) stated that the upper jaw is formed largely by the maxillary, and the figure of the type of *illustris* (McCulloch, *loc. cit.*, pl. 45, fig. 1) shows this bone to be proportionately somewhat longer than in Atlantic specimens examined. The maxillary is also proportionately longer in Matsubara's figures of *illustris* (1938, p. 42, fig. 4) and *surugaensis* (1943, p. 74, fig. 22). On the other hand, in Alcock's figure of the Indian Ocean *corythaeola* (Ill. Zool. Investigator, 1899, pl. 25, fig. 3) the premaxillary is nearly as long as the toothed portion of the maxillary, as it is in specimens at hand, and the same is true of Matsubara's figure of the Japanese *elongata* (1938, p. 45, fig. 5), Poll's figure of an eastern Atlantic specimen (1953, p. 58, fig. 23), and Smith's South African specimen (1949, p. 104, fig. 152). The relative

length of these two bones was not described for *africana* by Gilchrist and von Bonde (1924, p. 8, pl. 1, fig. 2) nor can they be distinguished in the figure of the type. Norman (1930, p. 289), who had both Australian and Indian Ocean specimens at hand, unhesitatingly synonymized *illustris* with *corythaeola* and his opinion should probably be upheld for the present.

Polymetme elongata (Matsubara) 1938, from Japan, is probably a distinct species. It differs from both *illustris* and *corythaeola* in having a smaller head, shorter snout and upper jaw, and lesser depth, as noted by Matsubara, and it may differ further, from *illustris* at least, in having a relatively longer premaxillary.

Yarrella blackfordi microcephala Matsubara (1941, p. 1) probably does not belong to the genus *Polymetme*. It differs in the following significant characters: tail very slender; anal origin beneath fifth dorsal ray; BR 8; OA 25, ending above fourth anal ray. It cannot, however, be assigned to any genus examined by me. In the position of the anal fin, the slender tail, and the number of BR and IV photophores it is like *Pollichthys*, but it differs from that genus in having a single ORB, two rows of teeth on the premaxillary, and ten pectoral rays (eight in *Pollichthys*). The species has not been figured.

Polymetme corythaeola (Alcock) 1898

Diplophos corythaeolum Alcock, 1898, Ann. Mag. Nat. Hist., (7) **2**: 147; 1899, Ill. Zool. Investigator, Fishes, pl. 25, fig. 3; 1902, Nat. Indian Seas, p. 239, fig. 38; Parr, 1931, Bull. Bingham Oceanogr. Coll., **2** (4): 12, 13.

Photichthys corythaeolus Alcock, 1899, Cat. Indian Deep-sea Fishes, p. 142; Brauer, 1906, Wiss. Ergebn. Deutschen Tiefsee Exp. Valdivia, **15** (1): 92, 374.

Yarrella africana Gilchrist and von Bonde, 1924, Rep. Fish. Mar. Biol. Surv. So. Afr., **3** (7): 8, pl. 1, fig. 2; Barnard, 1925, Ann. So. Afr. Mus., **21**: 148.

? Polymetme illustris McCulloch, 1926, Biol. Res. Endeavour, **5**: 167, pl. 45, fig. 1; 1929-30, Mem. Australian Mus., **5**: 51; Whitley, 1948, Fish. Bull. West. Australia Fish. Dept., **2**: 11.

Polymetme africana McCulloch, 1926, Biol. Res. Endeavour, **5**: 167; Barnard, 1927, Ann. So. Afr. Mus., **21**: 1018.

Polymetme corythaeolus McCulloch, 1926, Biol. Res. Endeavour, **5**: 167.

Yarrella corythaeola Norman, 1930, Discovery Rep., **2:** 289; Barnard, 1937, Ann. So. Afr. Mus., **32:** 46; Norman, 1939, Sci. Rep. John Murray Exp. 1933-34, **7** (1): 19; Bertin, 1939, Bull. Mus. Hist. Nat. Paris, **11:** 379; Herre, 1941, Mem. Indian Mus., **13:** 336; Smith, 1949, Sea Fishes So. Afr., p. 104, fig. 152; Misra, 1950, Rec. Indian Mus., **45:** 415; 1953, *op. cit.*, **50:** 398, fig. 17a; Poll, 1953, Rés. Sci. Exp. Océanogr. Belge (1948-1949), **4** (2), (3): 58, fig. 23; Springer and Bullis, 1956, Spec. Sci. Rep. U. S. Dept. Int., Fish., **196:** 50.

? *Yarrella corythaeola* Kamohara, *1936, Zool. Mag., Tokyo, **48.**

? *Yarrella illustris* Kamohara, 1938, Offshore Bottom Fishes Prov. Tosa, p. 9; Matsubara, 1955, Fish Morph. Heir., **1:** 221, pl. 16, fig. 61.

? *Yarrella blackfordi illustris* Matsubara, 1938, Jour. Imp. Fish. Inst. Tokyo, **33:** 42, fig. 4; 1940, Suisan Kenkiu-shi, **35:** 319; Kamohara, 1952, Rep. Kochi Univ. Nat. Sci., **3:** 16; Haneda, 1952, Pacific Sci., **6:** 13.

Yarrella blackfordi corythaeola Matsubara, 1938, Jour. Imp. Fish. Inst. Tokyo, **33:** 44.

Yarrella blackfordi africana Matsubara, 1938, *loc. cit.*

Yarrella blackfordi Longley and Hildebrand, 1941, Publ. Carnegie Inst. Washington, **535:** 15 (part); Springer and Bullis, 1956, Spec. Sci. Rep. U. S. Dept. Int., Fish., **196:** 50 (part).

? *Yarrella surugaensis* Matsubara, 1943, Jour. Sigen. Kenk., **1:** 74, fig. 22; 1955, Fish Morph. Heir., **1:** 221, pl. 17, fig. 63; Kamohara, 1957, Res. Rep. Kochi Univ., **6** (5): 1.

Photichthys argenteus Bruun, 1950, Atlantide Rep., **1:** 20, fig. 13.

The following western Atlantic specimens have been examined.

Gulf of Mexico: One specimen, standard length 125 mm., University of Miami Marine Laboratory No. 49:769, *Antilles*, 29° 13′ N., 88° 2′ W., 200 fathoms (366 meters).

Gulf of Mexico, *Oregon:* One specimen, 113 mm., Station 382, 29° 11.5′ N., 88° 07.5′ W., 21 June 1951, 190-210 fathoms (348-384 meters); five specimens, 74-112.5 mm., Station 1054, 19° 37′ N., 92° 40′ W., 15 May 1954, 200 fathoms (366 meters), 52°F. at bottom; two specimens, 86 and 127 mm., Station 1055, 19° 14′ N., 93° 00′ W., 15 May 1954, 225 fathoms (411 meters), 50°F. at bottom; two specimens, 195 and 207 mm., U.S.N.M. No. 157907, Station 1272, 28° 20′ N., 89° 46′ W., 8 March 1955, 250 fathoms (457 meters), 49°F. at bottom; one specimen, 145 mm., U.S.N.M. No. 157909, Station 1277, 28° 32′ N., 86° 20′ W., 11 March 1955, 260 fathoms (475 meters), 48°F. at bottom; one specimen, 113.5 mm., U.S.N.M. No. 157899, Station 1407, 28° 07′ N., 89° 59′ W.,

*Starred references not seen.

20 September 1955, 258 fathoms (472 meters); one specimen, 129 mm., U.S.N.M. No. 157898, Station 1412, 27° 58′ N., 90° 41′ W., 21 September 1955, 150-175 fathoms (274-320 meters), 53°F. at bottom; one specimen, 157 mm., Station 1541, 24° 28′ N., 83° 29′ W., 15 June 1956, 220 fathoms (403 meters); four specimens, 121-134 mm., Station 1565, 29° 11′ N., 88° 02′ W., 22 June 1956, 240 fathoms (438 meters), 52.2°F. at bottom; one specimen, 146.5 mm., Station 1566, 29° 13′ N., 87° 54′ W., 22 June 1956, 250 fathoms (457 meters); one specimen, 123 mm., Station 1963, 29° 11′ N., 88° 03′ W., 24 September 1957, 240 fathoms (438 meters).

Atlantic off Florida: One specimen, *ca.* 80 mm., U.S.N.M. No. 116937, Longley Collection (reported by Longley and Hildebrand, 1941, under the name *Yarrella blackfordi*); one specimen, 133.5 mm., *Combat* Station 446, 25° 10′ N., 79° 13′ W., 23 July 1957, 250 fathoms (457 meters), between Florida and the Bahama Islands.

Caribbean Sea: One specimen, 115.5 mm., collection of the Museum of Comparative Zoology, *Blake* Exp. 1880, off Cayman Brac, 247 fathoms (452 meters).

Western Caribbean Sea, *Oregon:* Three specimens, 113-140 mm., Station 1871, 16°39′N., 82°26′W., 22 August 1957, 250 fathoms (457 meters); four specimens, 85.5-*ca.*134 mm., Station 1872, 16° 41′ N., 82° 20′ W., 22 August 1957, 300 fathoms (548 meters); one specimen, 158 mm., Station 1888, 16° 41′ N., 81° 02′ W., 23 August 1957, 250 fathoms (457 meters); two specimens, 102 and 151 mm., Station 1889, 16° 39′ N., 81° 01′ W., 24 August 1957, 250 fathoms (457 meters); two specimens, *ca.* 146 and 147 mm., Station 1902, 11° 27′ N., 83° 11′ W., 9 September 1957, 135 fathoms (247 meters); six specimens, 123-*ca.*140 mm., Station 1903, 11° 31′ N., 83° 09′ W., 9 September 1957, 150 fathoms (274 meters); one specimen, 94 mm., Station 1919, 13° 30′ N., 82° 00′ W., 12 September 1957, 275-300 fathoms (503-549 meters); four specimens, *ca.* 49-189 mm., Station 1921, 13° 33′ N., 81° 55′ W., 13 September 1957, 275 fathoms (503 meters); one specimen, 134 mm., Station 1943, 16° 43′ N., 82° 44′ W., 16 September 1957, 275 fathoms (503 meters); seven specimens, 78-186 mm., Station 1945, 16° 41′ N., 82° 40′ W., 16 September 1957, 250-300 fathoms (457-549 meters).

Off northern South America: One specimen, *ca.* 63 mm., U.S.N.M. No. 44588, *Albatross* Station 2125, 11° 43′ N., 69° 09′ 30″ W., 18 February 1884, 208 fathoms (380 meters).

Off northern South America, *Oregon:* One specimen, *ca.* 108 mm., Station 1991, 09° 17′ N., 59° 19′ W., 4 November 1957, 250 fathoms (457 meters); four specimens, 83-152.5 mm., Station 1992, *ca.* 09° N., 59° W., 4 November 1957, 275 fathoms (503 meters); three specimens, 101.5-*ca.*140 mm., Station 2005, 07° 34′ N., 54° 50′ W., 6 November 1957, 200 fathoms (366 meters).

P. corythaeola was reported from the western Atlantic off Tortugas, Florida, by Longley and Hildebrand (1941, p. 15) under the name *Yarrella blackfordi* (see p. 88). The first Atlantic specimens were described by Poll (1953, p. 58) from West Africa, although Bertin (1939, p. 379) had earlier listed two specimens from the Cape Verde Islands, taken by the *Talisman.* Bruun (1950, p. 20) reported specimens under the name *Photichthys argenteus* Hutton, from the Gulf of Guinea, in either 530-850 or 650-260 meters. The position of the anal fin and the number and position of the lateral row of photophores (*loc. cit.,* p. 21, fig. 13) show these specimens to be *Polymetme corythaeola.* The species is otherwise known from South Africa, the tropical Indian Ocean, and possibly from the Pacific off Japan and Australia.

The following counts have been made on specimens examined: dorsal rays 11-13, anal rays 30-33, pectoral rays 10-11, ventral rays 7, branchiostegal rays 12-13, gill rakers on first arch 11-12 + 5. The photophores are large and conspicuous, their counts: BR 9; IV 9 + 1 + 11 = 21, the tenth elevated; VAV 8; AC 24-25, the first one or two slightly elevated and sometimes elongate, the last six or seven behind the anal fin; IC 53-54; OA 17 (an additional small, incomplete organ on one side of one specimen), not quite reaching a vertical from the anal origin.

There is some variation in the placement of the OA photophores. The first two are usually joined basally, i.e., the reflectors juxtaposed; two or three above the ventral fins are usually smaller, narrower, and irregularly disposed; and the last eight or nine are usually smaller and narrower, and sometimes a little higher than the pre-ventral organs. However, in

some specimens the first two OA are quite separate; in some, all of the OA are more or less equal in size and all on one level, and in one specimen the last eight organs are on a slightly lower level than the anterior ones. These variations occur at times on a single specimen, the left side differing slightly from the right.

No luminous tissue has been noted on the head or body of this species, but on most specimens there is a fragile tube of transparent skin on the belly between the ventral bases and the anus (below the VAV photophores), sometimes partially torn and probably lost in specimens lacking it. This structure is usually quite colorless but in large specimens it is sprinkled with minute black spots.

Small specimens have a proportionately longer head, larger eye, longer upper jaw and premaxillary, a shorter distance between the ventral and anal fins, and a narrower caudal peduncle. The young are also more compressed, and the body depth decreases more abruptly behind the head than in the adult. In specimens less than about 100 mm. in standard length the premaxillary and the toothed portion of the maxillary are about equal in length, while in older specimens the maxillary is always a little longer. The following measurements, in per cent of the standard length, are given in two groups, the first figures representing specimens with a standard length of more than about 115 mm. (fourteen, 118.5-207 mm.), the second groups of figures, in parentheses, representing specimens about 115 mm. or less (ten, 60.5-115.5 mm.).

Depth 14.8-17.9 (14.8-16.8); head 21.0-23.6 (23.6-*ca.* 26.0); snout 4.55-5.86 (5.1-6.16); orbit 4.2-4.83 (5.2-*ca.* 6.4); interorbital width at center of eye 3.93-4.8 (4.05-4.77); upper jaw 15.3-17.6 (18.2-19.1); premaxillary 7.0-8.4 (8.5-*ca.* 9.75); toothed portion of maxillary 7.7-9.17 (8.83-*ca.* 9.75); tip of snout to dorsal origin 46.4-49.6 (47.2-49.5), to anal origin 54.4-58.8 (54.6-57.5), to ventral bases 38.3-42.2 (*ca.* 38.3-42.5); distance between first anal ray and base of middle caudal rays 41.9-45.0 (42.3-46.0), last anal ray and base of middle caudal rays 12.1-16.7 (11.8-15.8), last dorsal ray and base of middle caudal rays 40.5-43.1 (39.0-42.5), last dorsal ray and adipose fin 17.9-20.2 (17.7-20.6), ventral base and anal origin 15.0-17.95 (12.7-16.0); least depth of caudal peduncle 5.8-6.65 (4.25-6.16); dorsal base 8.8-11.2 (8.9-*ca.* 10.75);

anal base 27.9-30.9 (28.1-*ca.* 31.9); pectoral length 11.8-17.5 (*ca.* 13.0 and 17.1-20.5); ventral length 7.95-9.77 (9.1-*ca.* 11.5).

Apparently the only character in which Atlantic and Indian Ocean specimens differ is in the number of anal rays, 30-33 in the Atlantic, 25-30 in the Indian.

Photichthys Hutton 1872

Phosichthys Hutton, 1872, Cat. Fishes New Zealand, p. 55, type species *Phosichthys argenteus* Hutton, 1872, Cook Strait, New Zealand.

Photichthys Hutton, 1873, Trans. New Zealand Inst., **5:** 10 (emended spelling); Günther, 1887, Rep. Sci. Res. Voy. Challenger, Zool., **22:** 177; Goode and Bean, 1895, Ocean. Ichth., p. 104; Collett, 1896, Bull. Soc. Zool. France, **21:** 94; Barnard, 1925, Ann. So. Afr. Mus., **21:** 149; McCulloch, 1926, Biol. Res. Endeavour, **5:** 166; Norman, 1930, Discovery Rep., **2:** 292; Smith, 1949, Sea Fishes So. Afr., p. 104.

Generic characters. Eye normal, moderate or large. Snout about equal to diameter of orbit. Interorbital width at center of eye about equal to diameter of orbit. Mouth large, slightly oblique; toothed edges of premaxillary and maxillary straight; maxillary nearly reaching preopercle. Premaxillary about half as long as toothed portion of maxillary. Angle of preopercle slightly acute. Teeth of upper jaw uniserial, premaxillary with one or two longer teeth and a few small ones; maxillary teeth all rather short, unequal, curving slightly inward. Lower jaw with several widely spaced longer teeth (as long as large premaxillary teeth); smaller teeth between the long ones except anteriorly, where there is an outer row of small, inwardly curved teeth. Vomer with one or two teeth on each side. Palatines each with a long row of unequal teeth. Pterygoids toothless or each with a small patch of minute teeth posteriorly. Tongue with or without a few small teeth at tip. Gill rakers 11 + 4-5 = 15-16 on first arch. Spines on inner edge of first gill arch short (a little longer near angle), one or two minute spines below a few anteriorly. No pseudobranchiae. Scales present, very deciduous. Anus near anal fin, beneath twelfth to fourteenth VAV photophore. Head and trunk more than twice as long as tail. Origin of dorsal fin about in middle of body length. Origin of anal fin well behind end of dorsal fin. Ventral bases slightly in advance of dorsal origin. Adipose fin small, above middle or anterior portion of anal fin. ORB 2, one near lower anterior margin of

eye, the other below its posterior margin; anterior one larger. OP 3, upper one level with upper border of pupil; lower two on same level, behind end of maxillary, anterior one slightly larger. SO present. BR 17-18. No additional photophores on head. Body with two rows of serial photophores; photophores present on isthmus. IV 24-25, straight. VAV 15-17. AC 16-18, straight, five to seven of them behind anal fin. IC 57-58. OA 33-34, reaching above front of anal fin (about over third AC photophore). No additional photophores and no luminous tissue on body as far as known. Fin rays: dorsal 12-13, anal 23-26, pectoral 9, ventral 6-7. Branchiostegal rays 20-21, no spines at bases. Vertebrae 51, including hypural (counted from X-ray photograph of one specimen).

Remarks. Photichthys is closely related to *Woodsia* but differs in higher meristic counts, in having the gill rakers more developed, and in body proportions. The generic diagnosis is based on three specimens from New Zealand (p. 65) and also on published accounts. In the specimens examined the palatine teeth are unequal in size, some of the anterior ones are enlarged, the posterior ones are all small, and a few are curved. There are two small patches of minute pterygoid teeth and a few tiny teeth on the tongue.

The genus contains only one species, *P. argenteus* Hutton, which is known from New Zealand and in the South Atlantic from *ca.* 32° S., 8° W. to Cape Point, South Africa.

Gonostoma Rafinesque 1810

Gonostoma Rafinesque, *1810, Ind. Ittiol. Sicil., p. 64; type species *Gonostoma denudata* Rafinesque, 1810, Mediterranean; Bonaparte, *1841, Icon. Fauna Ital., **3:** Cuvier and Valenciennes, 1849, Hist. Nat. Poiss., **22:** 278; Günther, 1864, Cat. Fishes Brit. Mus., **5:** 391; 1887, Rep. Sci. Res. Voy. Challenger, Zool., **22:** 172 (part, *Cyclothone* in synonymy); Moreau, 1891, Hist. Nat. Poiss. France, Suppl., p. 78; Goode and Bean, 1895, Ocean. Ichth., p. 93 (part, not *G. brevidens*); Jordan and Evermann, 1896, Bull. U. S. Nat. Mus., **47:** 578 (part; not *G. brevidens*); Collett, 1896, Bull. Soc. Zool. France, **21:** 94; Brauer, 1906, Wiss. Ergebn. Deutschen Tiefsee Exp. Valdivia, **15** (1): 70; Weber and de Beaufort, 1913, Fishes Indo-Austr. Arch., **2:** 120; Barnard, 1925, Ann. So. Afr. Mus., **21:** 143; Norman, 1930, Discovery Rep., **2:**

* Starred references not seen.

281; Fowler, 1936, Bull. Amer. Mus. Nat. Hist., **70:** 229; Lozano Rey, 1947, Mem. R. Acad. Cien. Madrid, Ser. Cien. Nat., **11:** 158; Smith, 1949, Sea Fishes So. Afr., p. 104; Misra, 1953, Rec. Indian Mus., **50:** 396; Mead and Taylor, 1953, Jour. Fish. Res. Bd. Canada, **10:** 570.

Sigmops Gill 1883, Proc. U. S. Nat. Mus., **6:** 256; type species *S. stigmaticus* Gill, 1883, equals *Gonostoma elongatum* Günther.

Neostoma Vaillant, in Filhol, *1884, Nature, Paris, **558**; 1888, Exp. Sci. Trav. Talis., Poiss., pp. 96, 385; type species *N. bathyphilum* Vaillant, 1884, 1888; Collett, 1896, Bull. Soc. Zool. France, **21:** 95.

Cyclothone Goode and Bean 1895, Ocean. Ichth., p. 99 (part, *C. bathyphila, C. elongata*); Jordan and Evermann, 1896, Bull. U. S. Nat. Mus., **47:** 581 (part, *C. bathyphila, C. elongata*); Collett, 1896, Bull. Soc. Zool. France, **21:** 94 (part, *C. grandis* Collett); Alcock 1899, Descr. Cat. Indian Deep-sea Fishes, p. 139 (part, *C. elongata*); Fowler, 1936, Bull. Amer. Mus. Nat. Hist., **70:** 222 (part, *C. bathyphilum*).

Generic characters. Eye normal, moderate or small. Snout longer than or about equal to diameter of orbit. Interorbital width at center of eye longer than or about equal to diameter of orbit. Mouth large, oblique; toothed edge of premaxillary straight or slightly concave; toothed edge of maxillary convex or nearly straight, nearly reaching preopercle. Premaxillary less than half as long as toothed edge of maxillary. Angle of preopercle acute. Teeth of upper jaw uniserial, longer teeth with smaller ones in interspaces. Lower jaw with a row of teeth similar to those of upper jaw and, anteriorly only, a very short outer row. Vomer usually with 1-2 small teeth on each side (absent in *denudatum*). Palatines each with a single row of teeth. A patch of teeth on pterygoids on each side and usually a few additional teeth posteriorly on roof of mouth. Tongue with or without teeth. Gill rakers 10-17 + 5-11 = 15-27 on first arch. Spines on inner edge of first gill arch moderate or long, a row of prickles or minute spines below each one. No pseudobranchiae. Scales present or absent. Anus nearer anal origin than ventral bases. Head and trunk about the same length as, or longer than, tail. Dorsal origin about in middle of body length or behind it. Anal origin opposite or in advance of dorsal origin. Ventral fins well ahead of dorsal origin. Adipose fin present or absent. ORB 1 (obsolete in *bathyphilum*). OP 2 or 3, lower anterior one often absent or obscured by bone (all obsolete in *bathyphilum*). SO

* Starred references not seen.

present (except in *bathyphilum*). BR 9 (not always visible on *bathyphilum*). No other photophores on head, but luminous glands or tissue usually associated with some of the photophores. Body with two rows of serial photophores, but in *bathyphilum* and *gracile* the upper row irregular and placed relatively high on sides; no photophores on isthmus. IV 11-16, prepectoral organs irregular or arched upward. VAV 3-10. AC 15-23. IC 32-43. OA 11-21, extending beyond ventral bases, first one or two elevated (irregular in *bathyphilum* and *gracile*). Additional photophores sometimes present on body. Luminous tissue usually present in the procumbent caudal rays, either dorsally, ventrally, or both. Fin rays: dorsal 10-18, anal 21-31, pectoral 9-13, ventral 6-8. Branchiostegal rays 10-14, spines present at inner bases of most of them. Vertebrae 37-40.

Remarks. *Gonostoma* is closely related to *Cyclothone*, from which it differs externally principally in dentition. It is also similar to *Bonapartia* in many respects (dentition, positions of dorsal and anal fins, most meristic characters).

There is much more variation among the species of *Gonostoma* than is found in any other genus of the family with the exception of *Diplophos*, which has been divided into two subgenera. However, all species of *Gonostoma* are held together by rather striking similarities and a division, even into subgenera, is considered inadvisable. The inter-relationships of the species are not clear, with the exception that *denudatum* and *atlanticum* are closely related; and one or two common characters are at times shared by species which seem otherwise not to be closely related. For example, the anus is typically situated close to the anal fin (below or close behind the penultimate VAV photophore) but in both *gracile* and *ebelingi* it is more remote from the anal origin, although never, as far as known, nearer the ventral bases. Similarly, a relatively short tail has until recently been characteristic only of the closely related species *denudatum* and *atlanticum*, but the newly discovered *ebelingi* is also a short-tailed form.

In most gonostomatid genera the presence or absence of an adipose dorsal fin is a distinctive character, but in *Gonostoma* this fin may be well developed (*elongatum, bathyphilum, ebelingi*), small (*denudatum*), or absent (*atlanticum, gracile*). In species whose life-histories are known, the adipose appears

relatively late in the developmental period, whereas in other gonostomatid fishes with an adipose fin it is present in very early stages.

Gonostoma is unique in showing considerable variation in the arrangement of the photophores. In other gonostomatid genera the position of the light organs is relatively constant. The reduction in size and number of these organs in *bathyphilum* is correlated with the greater depth of habitat of this species, but the irregular placement of the OA in *bathyphilum* and in *gracile*, the additional row of photophores near the dorsal profile of *gracile*, and the many minute organs found on *elongatum*, and possibly also on *bathyphilum*, represent a departure from the usual generic limits. The recent discovery of a new species, *ebelingi*, with ten VAV and twenty-one OA, further emphasizes the variability found in the genus, which is otherwise characterized by a short ventral-anal space containing no more than five VAV, and by having only eleven to fifteen OA.

The amount of scalation present is uncertain as the scales are usually extremely deciduous. The body of *denudatum* is normally full scaled and that of *atlanticum* may be also. Scales have never been reported on any specimen of either *bathyphilum* or *gracile*, and only rarely on *elongatum*. The latter, however, has scales on at least some portions of the body, although they are very deciduous.

The following key will serve to distinguish the species of *Gonostoma* but is not necessarily phylogenetic.

Key to the species of the genus Gonostoma

1a. Anus well ahead of anal origin, sometimes alomst midway between ventral bases and first anal ray. First 4-5 IV in an ascending line, 5th or 6th directly below 4th or 5th and level with those following it.

2a. Adipose fin present. Anal origin opposite or only slightly in advance of dorsal origin. Head and trunk noticeably longer than tail. VAV 9-10. OA 21, all but the first on the same level. No row of photophores near dorsal profile of body.

ebelingi, new species
Pacific

2b. Adipose fin absent. Anal origin noticeably in advance of dorsal origin. Head and trunk about same length as tail. VAV 3-5. OA 11-14, somewhat irregularly arranged. A row of widely separated photophores near dorsal profile of body.

gracile Günther 1878[1]
Pacific

1b. Anus close to anal origin. First 5-6 IV forming an upwardly arched arc, or reduced in number to 2 or 3 (***bathyphilum***).

3a. Photophores minute, obscure. ORB, OP and SO usually obsolete in adult. OA irregularly arranged, some rather high on sides. A few posterior pterygoid teeth much enlarged. Anal rays 21-24. IV 11-13. Gill rakers on first arch 15-17 + 9-11 = 24-27.

bathyphilum (Vaillant) 1888
Atlantic

3b. Photophores obvious, if not always conspicuous. ORB, OP and SO relatively well developed, a glandular mass present below upper OP. OA mostly on a single level low on sides, only the first one or two elevated. Pterygoid teeth all small, or a few of the posterior ones slightly enlarged. Anal rays 27-31. IV 14-16. Gill rakers on first arch 10-12 + 5-9 = 15-21.

4a. Body and head with numerous minute photophores (not always evident). A mass of glandular tissue associated with each SO and ORB. Gill rakers 10-12 + 7-9 = 18-21. Head and trunk almost same length as tail. Interspace teeth in jaws not especially close-set.

elongatum Günther 1878
Atlantic, Pacific, Indian

4b. No minute photophores on body or head. No glandular masses associated with ORB or SO (but a small silvery reflector present behind ORB). Gill rakers 10-11 + 5-6 = 15-17. Head and trunk noticeably longer than tail. Interspace teeth in maxillary close-set and about equal in size.

5a. Adipose fin present. Teeth absent on vomer, present on tongue centrally. First two AC photophores above, second two below remaining AC. Gill rakers 10 + 5 = 15.

denudatum Rafinesque 1810
eastern Atlantic, Mediterranean

[1]See Matsubara (1938, p. 41, fig. 3); Mead and Taylor (1953, p. 568). Synonym: *Gonostoma vitiazi* Rass (1950, p. 1041, fig.).

5b. No adipose fin. Teeth present on vomer, absent on tongue centrally.[1] First one or two AC photophores slightly elevated, others on one level. Gill rakers 11 + 5-6 = 16-17.

atlanticum Norman 1930
Atlantic, Pacific

Gonostoma atlanticum Norman 1930

Gonostoma denudatum atlanticum Norman 1930, Discovery Rep., **2:** 283; Atlantic, 8° 12′ N., 18° 49′ W. to 0° 56′ S., 14° 08′ 30″ W., type locality not designated.

Gonostoma denudatum Goode and Bean 1895, Ocean. Ichth., p. 98 (part, off northern Florida); Jordan and Evermann, 1896, Bull. U. S. Nat. Mus., **47:** 579 (part); Murray and Hjort, 1912, Depths of Ocean, pp. 604, 605, 612, 744, fig. 456 (middle and eastern Atlantic); Jespersen and Täning, 1926, Rep. Danish Oceanogr. Exp. 1908-1910, **2,** (A 12): 4 (part), fig. 2 (part) (Atlantic, *ca.* 12° N., 35° W.); Grey, 1956, Fieldiana, Zool., **36:** 119 (part); Koefoed, 1958, Rep. Sci. Res. M. Sars No. Atl. Deep-sea Exp. 1910, **4,** (2), (6): 13 (part?).

The following specimens have been examined.

Atlantic off Florida: One, standard length 53 mm., U.S.N.M. No. 44582, *Albatross* Station 2665, 29° 47′ N., 80° 05′ 45″ W., 4 May 1886, 263 fathoms (480 meters), 45.2° F. at bottom (reported by Goode and Bean, 1895).

Atlantic off South Carolina, one specimen, 63.5 mm., *Combat* Station 296, 32° 40′ N., 77° 40′ W., 21 April 1957, 220 fathoms (403 meters).

Western Pacific: Two, standard length *ca.* 55 and 46 mm., SIO 56-133, Marshall Island area, 12° 27′ N., 164° 30′ E. to 12° 38.8′ N., 165° 09′ E., 15-16 June 1956, *Horizon*, 10′ midwater trawl, 0-1150 fathoms (0-2104 meters).

Counts and proportions of these specimens are shown in Table 5.

Head and body considerably compressed. Skin entirely or almost entirely lost, no remains of scales or scale pockets except in smaller Pacific specimen, where there is evidence on the tail that scales were once present. Head and trunk longer than tail. No adipose fin. Anus below fourth VAV photophore, near anal origin. Spines on inner edge of first gill arch short.

[1]One minute tooth found on each lateral edge, posteriorly, in one specimen of *atlanticum*.

Edge of premaxillary straight, toothed edge of maxillary convex. Maxillary with a series of 9-10 longer teeth and 4-8 small, subequal, close-set teeth in each interspace except posteriorly; last four maxillary teeth slightly enlarged and without interspace teeth. Teeth of lower jaw similar but interspace teeth less close-set and slightly larger than those of upper jaw; anteriorly two to four small outer teeth and a few minute ones. Vomer with two very small teeth on each side, difficult to distinguish. Atlantic specimens with three or four teeth on each palatine, increasing in size posteriorly and followed by a few minute teeth; Pacific specimens with three teeth on each palatine, the second one largest. Pterygoids with a patch of very small teeth; none enlarged; none visible posteriorly in smaller Atlantic specimen, a few present in larger Atlantic specimen and in Pacific specimens. Tongue toothless except in larger Atlantic specimen, which has 1-2 minute teeth on each lateral edge posteriorly.

No gland tissue associated with ORB or SO, but a small, narrow silvery reflector present behind ORB. SO minute. OP 3, glandular material present below upper one, which is level with center of eye; lower two about level with end of maxillary, posterior one larger and slightly higher than anterior one. Photophores on body without evident glandular areas. Five prepectoral IV photophores forming a very low arc; first one or two AC slightly elevated, others on one level; OA all or nearly all lost in Atlantic specimens and in larger Pacific specimen, last three (behind ventrals) remaining on larger Atlantic specimen, in a slightly ascending line, ending over space between third and fourth VAV; smaller Pacific fish with 13 OA, the first elevated, the last three (behind ventrals) in an ascending line, ending above space between third and fourth VAV. Two infracaudal glands present in Pacific specimens, and larger Atlantic specimen with a small mass of tissue below last AC photophore, probably somewhat more extensive in life. No supracaudals (lost?).

Color of smaller Atlantic specimen pale yellowish brown after long preservation, peritoneum darker, inside of mouth and opercles pale. Skin remaining on larger Atlantic specimen blackish; end of peduncle blackish; fin rays colorless, base of each

dorsal and anal ray black, peritoneum black; inside of mouth with some black puncticulations; linings of gill covers and inner half of branchiostegal membranes black. Skin remaining on Pacific specimens blackish brown, cheeks silvery with black puncticulations, peritoneum and linings of opercles black, inside of mouth pale anteriorly and dusky posteriorly.

G. atlanticum was originally distinguished by Norman as a subspecies of *G. denudatum* Rafinesque on the basis of differences in the arrangement of the AC photophores and the number of gill rakers (usually 10 + 5 in *denudatum*, 11 + 6 in *atlanticum*). *G. atlanticum* is here given specific rank. It has been found to differ further from *denudatum* in lacking an adipose fin and tongue teeth, in being more slender bodied, in having a longer dorsal base, and in being a smaller species. Dr. D. W. Tucker has written (*in litt.*, 1958) that none of the specimens of the type lot, in the British Museum, has an adipose fin; and that a specimen 48 mm. in standard length, from *Discovery* Station 296, is a female with ovaries in which the eggs are readily distinguished, although not fully developed. The *Albatross* specimen has not been examined internally but the *Combat* specimen and both Pacific specimens reported here are also females with immature eggs in the ovaries.

G. atlanticum is known from the central and eastern Atlantic, from the latitude of the Azores (*ca.* 39° N.) south to 0° 56′ S., 14° 08′ 30″ W., off the African coast; and in the western Atlantic off the southern United States coast. In the Pacific it is known so far only from the two specimens reported here from the Marshall Island area. Norman's statement (1930, p. 283) that Goode and Bean reported *G. denudatum* off the coast of California was an error.

Goode and Bean (1895, p. 98) stated that *G. denudatum* was trawled off New England by the *Fish Hawk* in 1881, but no further data was given. In the same work, on page 102, these authors listed, under the name *Cyclothone elongata*, a specimen from *Fish Hawk* Station 1048, which was made on October 10, 1881. This specimen, U.S.N.M. No. 29069, cannot now be located but there is in existence an unpublished drawing of it, labeled "*Gonostoma denudata*, U.S.N.M. 29069, *Fish Hawk* Station 1048, H. L. Todd, del., Jan. 1882." The drawing undoubtedly

represents *G. elongatum* Günther and the record of *denudatum* from New England was perhaps an error based on an original mis-identification of this specimen.

Gonostoma ebelingi, new species

Holotype. Standard length 97 mm. Scripps Inst. of Oceanography No. SIO-56-133, Marshall Island area, 12° 27′ N., 164° 30′ E. to 12° 38.8′ N., 165° 09′ E., 10′ mid-water trawl, 1150-0 fathoms (2104-0 meters), *Horizon*, 15-16 June 1956, time 1725-0830.

Paratype. Standard length *ca.* 87 mm. Scripps Inst. of Oceanography No. SIO-56-127, same locality, 13° 03′ N., 166° 04′ E. to 13° 03′ N., 166° 32′ E., 10′ mid-water trawl, 400-0 fathoms (732-0 meters), 23-24 June 1956, time 2020-0700.

Description. Counts and proportions in parentheses refer to the paratype. Dorsal 13 (12). Anal 28 (28). Pectoral 9 (9). Ventral 8. Branchiostegal rays 13 (13), six (eight) of them with short spines at bases. Gill rakers 12 + 8 (11 + 8) on first arch. Number of vertebrae unknown.

Measurements in per cent of standard length, 97 (*ca.* 87) mm.: depth *ca.* 11.85; head *ca.* 22.7; snout 3.61; orbit 2.68; interorbital width at center of eye *ca.* 3.61 (*ca.* 3.45); upper jaw 18.05; premaxillary 5.15; toothed edge of maxillary 12.9; lower jaw *ca.* 18.6; tip of snout to dorsal origin 58.3 (*ca.* 59.8), to anal origin 58.3 (*ca.* 57.5), to ventral bases *ca.* 39.7 (*ca.* 40.2); distance between first anal ray and base of middle caudal rays 40.2 (*ca.* 38.8), last anal ray and base of middle caudal rays 8.76 (*ca.* 8.05), last dorsal ray and base of middle caudal rays 27.8 (*ca.* 27.0-27.6), last dorsal ray and adipose fin 7.74 (*ca.* 8.6), ventral base and anal origin *ca.* 18.05 (*ca.* 16.7); least depth of caudal peduncle 4.13 (*ca.* 4.0); dorsal base 12.4 (*ca.* 12.65); anal base 31.4 (*ca.* 33.3); ventral length 8.76.

Head and body considerably compressed. Neither specimen in perfect condition, head and body just behind head damaged in paratype, pectoral fins broken in both specimens, skin almost entirely lost in paratype, and with it most of the photophores of the lateral row. No scales or scale pockets visible. Head and trunk noticeably longer than tail. Anal origin behind middle of body length, below or slightly in advance of dorsal origin.

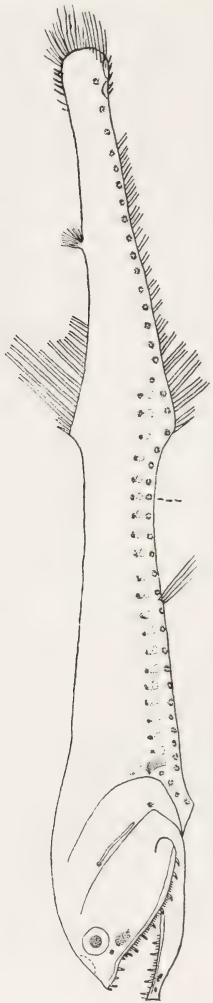

Figure 3. *Gonostoma chilingi*, new species. Holotype, Scripps Institution of Oceanography No. SIO 56-133. Standard length 97 mm.

Adipose fin moderate, short-based, situated above end of anal fin. Pectorals broken. Ventrals reaching fifth VAV photophore in holotype, broken in paratype. Anus beneath sixth VAV photophore, well ahead of anal origin.

Edge of premaxillary straight, toothed edge of maxillary convex. Eye moderate. Angle of preopercle acute. Spines on inner edge of first gill arch well developed but not quite half as long as longest gill raker.

Premaxillary teeth of holotype all broken off short; upper jaw lacking in paratype except the premaxillary of one side, this bearing seven teeth, one fang-like, the others smaller and of varying lengths. Longer teeth of maxillary mostly broken; interspace teeth numbering six to ten, small, about equal in size, evenly spaced and rather close together. Lower jaw with about nine long teeth; four to six smaller teeth in each interspace, unequal in size and not close together; anteriorly probably three or four teeth in outer row, mostly broken. Vomer with one small tooth on each side. Holotype with a row of about twelve small, well separated teeth on each palatine, smaller posteriorly; palatine bones of paratype broken, remaining teeth smaller than those of holotype. Pterygoid teeth all small, sparse, in a small patch anteriorly; posteriorly a few scattered teeth. Tongue without teeth.

Photophores moderate. ORB with a relatively large gland behind it, SO with a small one. OP 2, upper one small, level with center of eye, a narrow streak of glandular material below it; lower posterior one larger, level with end of maxillary; lower anterior one absent. BR 9. No separate glandular areas associated with ventral row of photophores on body; a small mass of gland tissue below each photophore of the lateral row. IV 15, first four rising toward pectoral base, fifth directly below fourth and on the same level as the remaining ten. VAV 10, continuous with AC. AC 19, all on one level except the third, which is slightly elevated; possibly an additional raised organ at base of caudal fin. IC 44. OA 21, the first elevated, others straight, reaching a vertical from sixth anal ray; almost all missing in paratype. Two infracaudal glands, no supracaudal (possibly lost).

Color brownish black, abdomen and branchiostegal membrane black. Traces of dark metallic iridescence on both head and body. Inside of mouth and gill covers dark.

Remarks. G. ebelingi is distinct from all other species of the genus *Gonostoma* in having a much greater distance between ventral and anal fins, a correspondingly larger number of VAV photophores, and more OA photophores. Within the genus its relationships are obscure. Only in *gracile* is the anus situated so far in advance of the anal origin and these two species are also similar in coloration, in the arrangement of the prepectoral IV photophores, and in having the OA extend beyond the anal origin. On the other hand, *ebelingi* is like *denudatum* and *atlanticum* in the relative proportions of trunk and tail, and in having the small interspace teeth of the maxillary close-set and more or less equal in size.

The species has been named for Dr. Alfred W. Ebeling, of Scripps Institution of Oceanography, in appreciation of his interest and assistance during the course of this study.

Danaphos Bruun 1931

Danaphos Bruun 1931, Vidensk. Medd. Dansk Naturh. Foren., **92:** 286.

Generic characters. Eye tubular, directed obliquely upward. Snout slightly shorter than orbit. Interorbital width at center of eye much less than diameter of orbit. Mouth moderate, nearly vertical; maxillary abruptly horizontal, its toothed edge convex, reaching or nearly reaching a vertical from posterior margin of eye. Premaxillary more than half as long as toothed edge of maxillary. Angle of preopercle slightly obtuse or nearly vertical. Teeth of upper jaw uniserial, minute on premaxillary; slightly longer on maxillary, very slender, much shorter teeth between longer ones. Teeth of lower jaw minute, seen under high power to be in two or more rows in anterior half of jaw, uniserial and slightly larger posteriorly. No teeth on vomer, palatines, pterygoids or tongue. Gill rakers 11-13 + 2 = 13-15 on first arch. Spines on inner edge of first gill arch rudimentary. Pseudobranchiae present but very small and fragile. Scales present but very deciduous. Anus a little nearer anal origin than ventral bases, beneath third or fourth VAV photophore. Head and trunk slightly shorter than tail. Origin of dorsal fin well ahead of

middle of body length. Origin of anal fin behind end of dorsal fin. Ventral bases beneath dorsal fin. Adipose fin present or absent; if present, small and poorly developed. ORB 1, in front of center of eye. OP 2 or 3, upper one not always present; lower two behind end of maxillary, about equal in size or the anterior one slightly larger. SO absent. BR (6). No additional photophores on head. Body with two rows of serial photophores; photophores present on isthmus. IV (3) + (4) + 1 + (2) + 8 = 18. VAV usually (5), (4) in one specimen. AC (3) + 14-18 + (4)[1] + 1 = 22-26, straight. IC 45-49. OA (2) + 4-5 = 6-7. No additional photophores and no luminous tissue on body as far as known. Fin rays: dorsal 6, anal 24-25, pectoral (12?) 13-14, ventral 6. Branchiostegal rays 9-10, bases prominent on inner edge and occasionally with minute spines. Vertebrae 38, counted on X-ray photograph of one specimen.

Remarks. As suggested by Bruun (1931, p. 287) *Maurolicus oculatus* Garman (1899, p. 241, pl. 53, fig. 3) belongs in the genus *Danaphos*. New material of this species from the eastern and northern Pacific has shown that *Danaphos asteroscopus* Bruun 1931, known from the tropical Indian Ocean and from the central and western parts of the Pacific, is probably a synonym of *D. oculatus*. The only apparent distinctions between the two species are the presence, in *asteroscopus*, of a small and poorly developed adipose fin, which could not be found on any of the specimens examined; and the fact that *asteroscopus* was said to have an upper OP photophore, which is not present on any of the specimens seen. Many of the latter are mature, or nearly so, both sexes being represented but females predominating. The generic description was based on the following specimens of *D. oculatus* from the collection of Scripps Institution of Oceanography.

Eastern Pacific: Two, standard length 33 and 36 mm., SIO 54-98, 26° 23.5′ N., 123° 14′ W., to 26° 53.5′ N., 123° 22′ W., 25-26 June 1954, 10′ midwater trawl, 1578 fathoms (2886 meters); five, standard length 28-38 mm., SIO 57-43, 28° 52′ N., 118° 12.5′ W. to 28° 59.5′ N., 118° 09′ W., 10 February 1957, 380-0 fathoms (695-0 meters); eleven, standard length 32-39 mm., SIO 57-206, 28° 34.5′ N., 126° 52′ W. to 28° 47.9′ N., 126° 24′ W., 20-21 June

[1]One specimen with (3) on left side, (4) on right side.

1955, 10′ midwater trawl, 0-675 meters; sixteen, all fragmentary, SIO 57-88, 28° 46′ N., 126° 33′ W. to 28° 17′ N., 126° 45′ W., 22 May 1955, 10′ midwater trawl, 0-348 fathoms (0-636 meters); two, standard length *ca.* 29 and 26.5 mm., H-51-188, 33° 09′ N., 118° 01′ W. to 32° 57′ N., 117° 48′ 30″ W., 22 May 1951, 200 fathoms over 490-500 fathoms (360 meters over 896-1006 meters).

North Pacific: Nineteen, standard length 21-39 mm., H 51-354, 40° 23′ N., 139° 23′ W., 5 August 1951, 10′ midwater trawl, 400-650 meters; thirteen, standard length 21-43 mm., H 51-358, 40° 35′ N., 147° 55′ W., 10 August 1951, 10′ midwater trawl, 350-600 meters; fifteen, standard length 27-*ca.* 45 mm., H 51-359, 41° 42′ N., 150° W., 11 August 1951, 600-800 meters.

Neophos Myers

Neophos Myers, 1932, Copeia, p. 61.

Generic characters. Eye normal, moderate or large. Snout shorter than orbit. Interorbital width at center of eye less than diameter of orbit. Mouth large, oblique; premaxillary nearly vertical, its toothed edge straight; toothed edge of maxillary curving abruptly downward from juncture with premaxillary, becoming almost straight posteriorly, nearly reaching preopercle. Premaxillary about half as long as toothed portion of maxillary. Angle of preopercle vertical. Teeth all minute, irregular on premaxillary, uniserial and with some slightly longer teeth on maxillary; teeth of lower jaw uniserial but with a short outer row of minute teeth anteriorly. Vomer with a few teeth on each side. Palatines each with a few teeth. No teeth on pterygoids or tongue. Gill rakers about 13-14 + 5 = 18-19 on first arch. No spines on inner edge of first gill arch, a few minute ones on second arch. Pseudobranchiae present. No evidence of scales. Anus close to anal origin, beneath last VAV photophore. Head and trunk shorter than tail. Origin of dorsal fin about in middle of body length. Anal origin well ahead of dorsal origin. Ventral bases well ahead of dorsal origin. No adipose fin. ORB 1, in front of eye. OP 3, upper one elongate, about level with middle of eye; lower two on the same level behind end of maxillary, the posterior one larger. SO present. BR (6). No additional photophores on head. Body with one row of serial photophores and a single organ representing the lateral row; photophores

present on isthmus. IV 1 + (2) + (3), on isthmus, + 11 = 17. VAV 1 + (3) + 1 = 5. AC 13, all single, straight, two of them behind anal fin. IC 35. OA 1, above pectoral base. No additional photophores and no luminous tissue on body as far as known. Fin rays: dorsal 8, anal 38, pectoral 13, ventral 7. Branchiostegal rays 7 or 8, no spines at bases. Number of vertebrae unknown.

Remarks. The type and only known specimen of *Neophos nexilis* Myers (1932, p. 61) has been examined. The genus is closely related to *Thorophos* Bruun and is possibly synonymous with it, but comparative material is necessary to establish their identity.

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Table 1.

Counts and proportions of Atlantic specimens of *Diplophos taenia*, taken from the literature where indicated.

	Lütken, 1892, p. 278	Brauer, 1906, p. 89	USNM No. 100525	USNM No. 100616	Lütken, 1892, p. 279
Locality	10° N., 12° and 25° W.	*ca.* 5° N., 13° W.	*ca.* 30° N., 66° W.	*ca.* 25° N., 77° W.	20° N., 50° W.
Dorsal rays	*ca.* 9	11	11	10	9
Anal rays	*ca.* 43	61	68	68	*ca.* 60
Pectoral rays	*ca.* 8	8	—	8-9	10
Ventral rays	*ca.* 8	8	—	7	8
Gill rakers on first arch	—	—	7 + 3	8 + 3	—
BR	—	15-16[2]	12-13	13-14	11-12[3]
IV	49	44	47	47	44
VAV	16	16	17	16	17
AC	43 + 2	43 + 2	47 + 2	46 + 2-3	47 + 2
IC	110	105	113	111-112	110
OA	*ca.* 72	70	73	71	*ca.* 68?
Lat. line	*ca.* 90	91	—	98	—
Standard length	41[1]	59	66	74	85
			Per cent of standard length		
Depth	7.3	10.2	8.2	8.25	8.25
Head	15.8	17.0	16.7	14.8	14.1
Snout	—	5.1	4.1	3.9	—
Orbit	—	3.4	2.4	2.3	2.35
Upper jaw	—	—	11.1	10.4	—
Interorbital width at center of eye	—	3.4	2.7	2.3	—
Tip of snout to:					
dorsal origin	48.8	47.5	45.5	46.0	47.0
anal origin	51.2	51.0	50.0	48.6	49.5
ventral bases	39.0	38.1	36.4	36.5	36.5
Anal origin to caudal base	—	—	50.5	52.9	—
Dorsal base	—	4.75	*ca.* 3.03	4.6	—
Anal base	—	45.0	50.0	50.7	—
Least depth of caudal peduncle	—	3.4	1.96	2.03	—

[1]Possibly total length. [2]See p. 78. [3]Counted on figure 2 of Plate 2.

Table 2.

Counts and proportions of Pacific specimens of *Diplophos*, taken from the literature where indicated.

	pacificus Günther, 1889, type	SIO 56-127	*"taenia"* Herre and Herald, 1950	*proximus* Parr, 1931, type	*Diplophos* sp., Scripps Inst. of Oceanogr.	*orientalis* Matsubara, 1940, type	*orientalis*, Abe, 1958
Locality	Mid-Pacific	Marshall Ids.	Sulu Sea	Eastern Pac.	Eastern Pac.	Japan	Japan
Standard length	37	*ca.* 40	34 41[3]	82+[4]	89-100	179.8	177
Dorsal rays	12	11	10-11	10	9-10	12	12
Anal rays	53	51?	59-61	58	55-60	63	*ca.* 63
Pectoral rays	9	9	9	9	9	10	10
Ventral rays	7	—	—	8	7-8	8	8
Gill rakers on first arch	—	—	—	9+?	9+3	9+3	9+3
BR	—	12	—	11	10-11[5]	—	11
IV	—	*ca.* 43	—	41	41-42	40	40
VAV	—	15	—	13	14-15	15	14
AC	—	44 + 2	—	41+2	40-42+2	39+4	39+[3?]
IC	—	*ca.* 104	97-103	95+	98-102	98	96+
OA	—	67	66-69	77-78	60-84	87	63+[8]
Lateral line	41[1]	89[2]	89-92	*ca.* 80	86[6]	86	67+(89?)[9]
			Per cent of standard length				
Depth	—	*ca.* 8.75	—	10.5	9.5-10.5	12.3	12.1
Head	—	*ca.* 16.25	—	16.5	18.0-18.1	16.8	17.2
Snout	—	*ca.* 5.0	—	4.5	3.5-4.1	3.9	4.4
Orbit	—	*ca.* 2.5	—	3.5	3.0-3.6	3.8	3.5
Interorbital width at center of eye	—	*ca.* 2.5	—	3.0	3.0-3.1	3.25	3.8
Upper jaw	—	*ca.* 12.5	—	11.5	11.4-11.5	11.7	12.1
Tip of snout to:							
dorsal origin	—	*ca.* 43.7	—	48.0	46.5-47.6	45.5	46.3
anal origin	—	*ca.* 47.5	—	50.0	50.8-51.0	—	—
ventral bases	—	*ca.* 37.5	—	37.0	36.5-38.4	—	37.9
Anal origin to caudal base	—	*ca.* 47.5	—	—	49.2-50.0	48.4	47.6
Dorsal base	—	—	—	—	4.6-5.0	5.85	6.2
Anal base	—	—	—	—	45.0-46.0	44.0	43.5
Least depth of caudal peduncle	—	—	—	—	2.0 2.1	2.78	3.1

[1]From figure. [2]To end of anal fin. [3]Total length. [4]Tip of tail lacking. [5]Also 1-3 minute photophores. [6]One specimen only. [7]One or two possibly lost. [8]Probably lost on latter half of tail. [9]Judging from figure, probably originally *ca.* 89, including those now lost.

Table 3.

Counts and proportions of *Yarrella blackfordi* and *Yarrella argenteola*.

	blackfordi	*argenteola*
Standard length, mm.	170-261	125-133
Dorsal rays	14-16	14
Anal rays	29-31	28-29
Pectoral rays	8-9	9
Ventral rays	7	7
Branchiostegal rays	14-16	13
Gill rakers on first arch	12-13+6-7=18-20	15-16+6=21-22
Vertebrae (from X-ray photographs)	54	45
BR	12-13	11-12
IV	9+3-4+11-12=23-25	9+3+11-12=23-24
VAV	12	9-10
AC	25-27	20-21
IC	61-63	52-53
	Per cent of standard length	
Depth	11.4-14.3	15.0-15.1
Head	20.5-23.8	22.5
Snout	4.4-5.4	5.6-6.0
Orbit	2.47-3.25	4.0-4.5
Interorbital width at center of eye	5.0-5.75	5.2
Upper jaw	15.2-17.7	16.5-17.2
Premaxillary	8.4-10.0	8.6-9.2
Toothed portion of maxillary	6.6-7.65	7.9-8.0
Tip of snout to:		
dorsal origin	49.5-51.7	54.0-54.2
anal origin	56.1-58.5	58.5-59.0
ventral base	37.2-40.1	40.1-40.8
Ventral base to anal origin	16.4-18.0	17.6-18.5
Anal origin to base of middle caudal rays	41.9-45.4	40.5-41.4
End of anal to base of middle caudal rays	15.5-18.6 (20.2)	13.9-14.0
End of dorsal to base of middle caudal rays	35.0-35.8	31.6
Dorsal base	11.3-12.6	14.0-15.0
Anal base	(21.4) 24.3-26.7	26.8-27.0
Least depth of caudal peduncle	6.4-7.3	6.4

Table 4.

Counts and proportions of *Triplophos hemingi*, taken from the literature where indicated.

	McArdle, 1901 Lloyd, 1909 Norman, 1930	Brauer, 1906	Poll, 1953	Western Atlantic specimens
Locality	Bay of Bengal	South of Ceylon	West Africa, 5°-11° S.	Caribbean and Surinam
Standard length	205 and ?	144	60-161	106-176
Dorsal rays	10	10	10-11	10-11
Anal rays	57-61	57	54-56	57-63
Pectoral rays	10-11	10	—	9-10
Ventral rays	6 (9?)	6	—	6-7
Branchiostegal rays	14	17	—	11-13
Gill rakers on first arch	—	—		14-16+9
BR	—	13	—	8-10
IV	29-30	30	—	24-25
VAV	5	5	5-7	7
AC	35-36	41	—	37-39
IC	69-71	76	—	68-70
	Per cent of standard length			
Depth	—	12.8	—	*ca.* 12.0-15.0
Head	—	14.6	—	*ca.* 15.0-17.5
Snout	—	1.39	—	*ca.* 1.7-2.8
Orbit	—	2.43	—	2.4-3.4
Interorbital width at center of eye	—	2.78	—	2.3-2.9
Tip of snout to:				
dorsal origin	—	27.8	—	29.6-31.5
anal origin	—	33.3	—	35.2-37.9
ventral bases	—	25.7	—	24.7-28.4
Least depth of caudal peduncle	—	2.08	—	1.3-1.9
Dorsal base	—	5.55	—	*ca.* 5.7-6.8
Anal base	—	64.0	—	60.0-*ca.* 61.5

Table 5.

Counts and measurements of *Gonostoma atlanticum*.

	Combat specimen South Carolina	U.S.N.M. 44582 Florida	SIO 56-133 Marshall Ids.	
Standard length	63.5	53	55	46
Dorsal rays	18	16	17	17
Anal rays	30	*ca.* 29	28	28
Pectoral rays	10	—	11	10?
Ventral rays	6?	—	7	—
Branchiostegal rays	11	11	11	11
Gill rakers on first arch	11+6	11+6	11+5	11+6
Vertebrae	—	38	—	—
BR	9	9	9	9
IV	15	16	16	16
VAV	5	5	5	5
AC	19	19	17+[1]	19
IC	39	40	—	40
OA	—	—[2]	—	13
	Per cent of standard length			
Depth	15.75	*ca.* 16.0[3]	*ca.* 16.3	*ca.* 16.3
Head	*ca.* 23.6	*ca.* 24.5	*ca.* 25.5	27.2
Snout	3.94	3.77	3.64-4.54	*ca.* 4.34
Orbit	*ca.* 3.94	3.77	4.54	4.34-5.43
Interorbital width at center of eye	3.94	3.77	4.54	3.26-4.34
Upper jaw	18.9	18.8	20.0	20.6
Premaxillary	3.94	3.77	4.54	4.34
Toothed portion of maxillary	15.0	15.1	15.4	16.3
Tip of snout to:				
dorsal origin	58.3	59.4	59.0	*ca.* 56.5
anal origin	58.3	57.5	56.5	*ca.* 55.4
ventral bases	*ca.* 48.8	47.1	*ca.* 47.2	*ca.* 46.7
Distance between:				
anal origin and caudal base	42.5	41.5	41.0	42.4
last anal ray and caudal base	9.45-10.0	11.3	*ca.* 10.0	9.77
last dorsal ray and caudal base	23.6	24.5	23.6	23.9
inner insertion of ventral base and anal origin	*ca.* 9.45	9.43	*ca.* 6.36	*ca.* 7.6
Least depth of caudal peduncle	6.3	5.65	6.36	5.43-6.5
Dorsal base	18.1-18.9	*ca.* 17.9	16.3-17.3	18.45
Anal base	33.1	31.1	*ca.* 29.8	*ca.* 32.6

[1]Lacking on end of tail.

[2]Unpublished drawing of this specimen, prepared in June, 1886, shows 13.

[3]Depth somewhat greater in drawing.

Table 6.

Meristic characters of gonostomatid genera.

Genus	Vertebrae	Dorsal rays	Anal rays	Pectoral rays	Ventral rays	Branchiostegal rays	Gill rakers on first arch
Diplophos (subgenus *Diplophos*)	*ca.* 85+?	9-12	53-68	8-10	7-8	11-14	7-9+3=10-12
Diplophos (subgenus *Manducus*)	63	12-13	36-41	10-11	7-8	11-13	8-9+3-5=12-14
Yarrella	45-54	14-16	28-31	8-10	6-7	13-16	12-16+6-7=18-22
Triplophos	*ca.* 60	10-12	54-63	9-11	6-7	11-14	14-16+9=23-25
Polymetme	45	11-13	24-33	9-11	7 (8?)	12-14	9-12+5-8=15-19
Pollichthys	*ca.* 40	10-12	22-30	8	6-7	11-12	11-12+4-5=15-17
Vinciguerria	38-42	13-16 (10?)	12-17 (10?)	9-10	7	10-12	11-23+3-11=15-33
Photichthys	51	12-13	23-26	9	6-7	20-21	11+4-5=15-16
Woodsia	?	12	14	9-10	7-8	17	2-4 at angle[1]
Ichthyococcus	38-47	10-15	13-17	7-8	6-7	11-12	15-26+7-11=22-37
Bonapartia	37	17-20	29-31	14-16	7-8	13-16	11-12+5-6=16-18
Margrethia	34	15-16	21-26	13-14	8	13	10+5=15
Gonostoma:							
denudatum	38-39	16-17	29-31	11-12	8	13-14	10+5=15
atlanticum	38	16-18	28-30	10-11	7	11	11+5-6=16-17
ebelingi	?	12-13	28	9	8	13	11-12+8=19-20
gracile	41	10-14	26 (?)-29	9-10	7-8	10-11	13-14+7-8=20-22
elongatum	39	12-14	29-32	10-12	8	12-13	11-12+7-9=18-20
bathyphilum	37	12-14	22-26	10-11	7-8	12-13	15-17+9-11=24-27
Cyclothone	29-33	12-15	16-21	9-13	6-7	10-14	9-18+4-10=14-27 (30)
Neophos	?	8	38	13	7	7-8	*ca.* 13-14+5=18-19
Thorophos	?	11	31	*ca.* 14	*ca.* 7	?	?
Danaphos	38	6	24-25	13-14	6	9-10	11-13+2=13-15
Valenciennellus	32-33?	7-12	22-25	12-13	6-9	9-10	12+2=14
Sonoda	40	8-9	22-25	13-15	6	8	15-18+3=18-21
Maurolicus	33-35	9-12	19-27	17-20	6-7	9-10	17-22+4-8=23-30
Argyripnus	46	10-14	22-27	15-19	7	8-10	15-17+5-7=22-24

[1]Total number of rakers and rudiments 13+3-5=16-18.

Table 6. (*Cont.*)

Meristic characters of gonostomatid genera.

Genus	Photophores					
	BR	IV	VAV	AC	IC	OA
Diplophos (subgenus *Diplophos*)	10-12+0-3	40-49	13-17	43-49	97-113	66-87
Diplophos (subgenus *Manducus*)	8-9	30-33	12-14	28-30	70-75	45-48
Yarrella	11-13	23-25	9-12	20-28	52-64	*ca.* 50+
Triplophos	8-13	24-30	5-7	35-41	68-76	50-56
Polymetme	9-10	19-21	7-8	21-25	50-54	16-18
Pollichthys	8	21-23	7-9	18-21	47-50	19-21
Vinciguerria	8	21-24	7-11	12-15	42-49	21-25
Photichthys	17-18	24-25	15-17	16-18	57-58	33-34
Woodsia	14	25	11-12	12	48-49	29-31
Ichthyococcus	11-12	25-28	9-14	12-14	46-55	23-31
Bonapartia	11-13	14-16	5	18-20	37-41	—
Margrethia	9-12	13-15	4	17	35-36	- -
Gonostoma:						
denudatum	9	15-16	5	17-20	37-41	13-15
atlanticum	9	15-16	5	19	39-40	13
cbelingi	9	15	10	19	44	21
gracile	9	15	3-5	17-19	35-39	11-13
elongatum	9	15	4-5	21-23	41-43	13-15
bathyphilum	9	11-12	4-5	20-21	35-37	14
Cyclothone	8-11	12-14	4-5	12-16	29-34	6-10
Ncophos	(6)	1+(2)+(3)+11=17	1+(3)+1=5	13	35	1
Thorophos	(6)	(6)+11=17	(5)	3+(2)+7+1 *or* (2)+1=14-15	36-37	(2)+5=7
Danaphos	(6)	(3)+(4)+1+(2)+8=18	(5)	(3)+14-18+(4)+1=22-26	45-49	(2)+4-5=6-7
Valenciennellus	(6)	(3)+(4)+(16-17)=23-24	(4-5)	9-16[2]	37-44	(2) *or* (2)+3=5
Sonoda	(6-7)	(6)+(10)=16	(7-8)	(16-21)+(19-24)=36-43	59-67	(2)+4-5=6-7
Maurolicus	(6)	(6)+(12-13)=18-19	(6)	1+(14-18)+(7-9)=22-27	46-52	(2)+7=9
Argyripnus	(5-6)	(6)+(10)=16		(18-28)+(5)+(12-18)=39-51[3]	53-67	(4)+3=7 *or* 7

[2]In 3-6 groups of very small organs, 2-4 per group.

[3]VAV and first group of AC continuous.

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TRICHECODON HUXLEYI (MAMMALIA: ODOBENIDAE) IN THE PLEISTOCENE OF SOUTHEASTERN UNITED STATES

By Clayton E. Ray

With Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March, 1960

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No. 3 — Trichecodon huxleyi (*Mammalia: Odobenidae*) *in the Pleistocene of southeastern United States*

By Clayton E. Ray

In 1877 Joseph Leidy (pp. 214-216, Pl. 30, fig. 6) described and illustrated the tusk of a fossil mammal from the Ashley River phosphate beds, near Charleston, South Carolina. He referred the specimen, with reservations, to the modern Atlantic walrus. This tentative Pleistocene record for the modern walrus, together with its climatic implications, has been accepted uncritically by biogeographers and paleoecologists to the present day (cf. Deevey, 1949, p. 1375; Dorf, 1959, pp. 184, 196). Recently, my own attempts to identify a fossil tusk (University of Florida No. 3274) found near Sarasota, Florida, have led me to re-examine the South Carolinian and other occurrences of fossil walruses. Aside from the living walrus, here treated as a single species (cf. Scheffer, 1958, p. 84; Davies, 1958, p. 102), and Quaternary specimens clearly pertaining to it,[1] the only form with which the Sarasota specimen can be compared usefully is *Trichecodon huxleyi* Lankester 1865,[2] from the Pleistocene of Europe. The tusks of other extinct forms are either unknown (*Prorosmarus*) or poorly known (*Alachtherium;* Hasse, 1910, p. 303).

DESCRIPTION

Judging from its slight curvature in the frontal plane, which, although variable, is characteristically mesad in walruses, the Sarasota specimen is apparently from the right side and will be so considered for purposes of description. The dimensions of the specimen are given in Table 1. The natural surface of the tusk is composed of a thin, smooth layer of cementum, still preserved

[1] These include, with the exception of the record for the Ashley River, those records cited by Kellogg (1922, pp. 49-51, *Trichecodon* was then considered to be Pliocene) and by Hay (1923, pp. 21-29), together with more recent reports by Allen (1930), Borissiak (1930), Dow (1954), Handley (1953), Matsumoto (1926), Norton (1930), and Palmer (1944).

[2] Lankester (1880, pp. 213-216) has shown beyond doubt that the name *Trichecodon* rests with his East Anglian fossils and not with the Belgian material of van Beneden (1877). Whether *Trichecodon* is congeneric with *Odobenus* must be determined on the basis of the European material, and is thus outside the scope of this paper.

Table 1. Measurements of tusk of *Trichecodon huxleyi* from Florida, U.F. 3274.

	mm.
Length along outer curve	435.0
Length in straight line	406.0
Greatest anteroposterior diameter	93.0
Greatest transverse diameter	56.9
Ratio of greatest transverse diameter to greatest anteroposterior diameter	.61
Greatest circumference	240.0
Least anteroposterior diameter	55.3
Least transverse diameter	34.3
Least circumference	90.8
Maximum thickness of cementum preserved	2.6
Long diameter of pulp cavity at proximal end	68.0
Short diameter of pulp cavity at proximal end	28.9
Long diameter of osteodentinal tube at distal end (estimated)	25.5
Short diameter of osteodentinal tube at distal end (estimated)	9.3
Depth of open pulp cavity (minimum)	60.0

for the most part. The dominant surface features are two strongly developed longitudinal grooves on the flattened medial surface (Plate 1A), both of which diminish in depth distally to the point of disappearance at the extreme tip of the tusk, perhaps due in part to wear. A similar, but weaker, groove is present on the posteromedial surface of the tusk. On the lateral, convex side are several lesser longitudinal grooves, largely smoothed out on the surface, but clearly shown where the cementum is missing (Plate 2). The cementum is thick in the grooves and thin on the intervening ridges, the effect of which is to mask the grooves. This condition is probably due to differential wear rather than to an initial variation in thickness of cementum deposited. The ridges are exposed to, and the grooves protected from, wear. The cementum is sharply differentiated by weathering into a firm, black, inner layer of variable thickness (owing to the fluting) and a flaky, gray, outer layer averaging 1-1.5 mm. in thickness. A small area of the extremely smooth outer surface of the unweathered layer is exposed by the exfoliation of weathered cementum at the distal extremity of the tusk (Plate 1B). At least some of the subsurface flutings persist to the distal extremity of the tusk as revealed in section at the broken distal

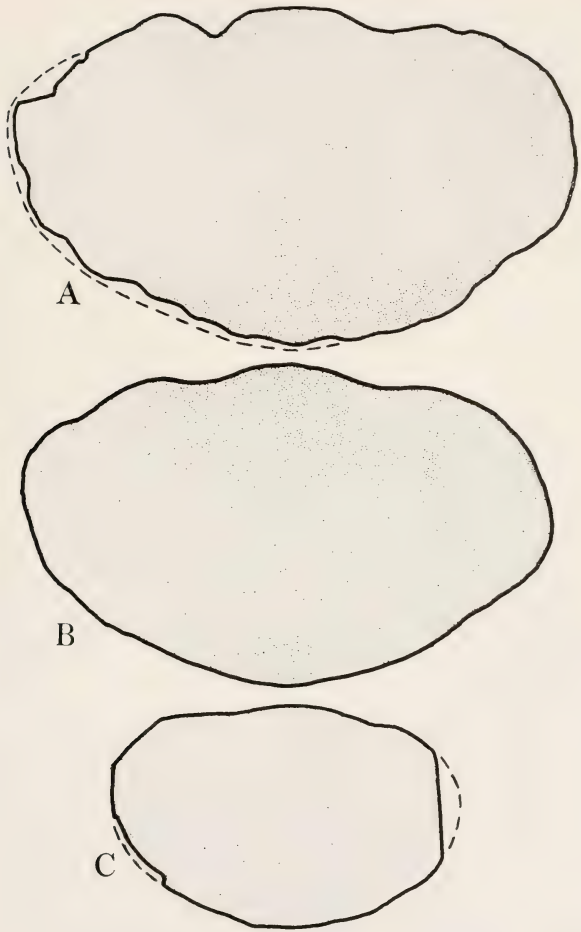

Figure 1. Transverse sections A, B, and C of U.F. 3274 at the points A, B, and C respectively, indicated on Plate 1B. The medial surface is upper, and anterior is to the right in each section. x1.

end. The fluted dentinal surface is marked by transverse striations or growth lines, which appear in Plate 2 as alternating light and dark bands (owing to the presence of light colored clay in the valleys between ridges), averaging about 9-10 of each per centimeter. The shape of the transverse section of the tooth is roughly that of a flattened ovoid with the medial side plano-convex and deeply grooved and the lateral side smoothly convex (Fig. 1). The tusk is rather strongly curved in the parasagittal plane. Its inner curvature forms an arc of a circle with a radius of about 45 centimeters, and its outer, of about 40 centimeters. These figures represent only the crudest of approximations, since the curvature is not constant throughout the length of the tusk. The degree of external curvature is strongly increased in the distal 10 centimeters of the tusk, as a result of natural wear which produced a flattened facet on the outer curvature (Fig. 1C). The tusk is also curved very gently mesad. The base of the open pulp cavity is occupied by a projecting mass of globular osteodentine (Plate 2), which fills the cavity solidly distad from the base, as revealed at the fractured distal end of the tooth. The tooth tapers abruptly distad, a feature enhanced by the wear on the outer curvature. Except for the distal 10 centimeters of the tooth, the curvature and taper shown represent very nearly the initial, unworn condition. If either feature were due largely to wear, the osteodentine would be exposed on the outer curvature of the tooth (cf. Lankester, 1880, p. 219, figs. 1, 2, and Mansfield, 1958, p. 26, fig. 5). The small amount of wear, deep, open pulp cavity, and unconstricted proximal end indicate that the tooth belonged to a subadult or adult (but not senile) individual.

The general form and structure together with the characteristic globular osteodentine leave no doubt that the tooth belongs to a walrus-like mammal. The presence of osteodentine, the ovoid cross-section, and the absence of "engine-turning" in the dentine rule out the possibility of its belonging to a proboscidean. However, certain discrepancies prevent the assignment of the tusk to *Odobenus rosmarus*. Although it is not certain that the true outer surface is anywhere preserved in the fossil, the sheath of cementum is apparently thinner than that of *O. rosmarus*. The maximum thickness of cementum measurable on the fossil is 2.6

mm.; that of a sectioned tusk of *Odobenus rosmarus* (M.C.Z. 21638), 4.0 mm. The maximum anteroposterior diameter of the fossil tusk is 10 millimeters greater than that of any modern walrus in the Museum of Comparative Zoology (19 adult individuals). Its maximum circumference equals that of the world's record Atlantic walrus and is exceeded only by the first and second-place Pacific walruses (Webb, et al., 1952, pp. 155, 158). These latter two individuals may be taken as approaching the absolute maximum in robustness for *Odobenus rosmarus,* since they represent maxima obtained from the world's major collections. It is improbable that the fossil lies at the upper size limit of its species. The deep, persistent, longitudinal surface grooves on the medial face and the fluting of the dentinal surface on the lateral face cannot be matched in *O. rosmarus.* The transverse striations are not interspersed with widely separated, strong, transverse (annual?) ridges, as they are in *O. rosmarus* (cf. Brooks, 1954, p. 40, fig. 7, and Mansfield, 1958, p. 31, fig. 7, p. 35, fig. 8A). The fossil is more flattened transversely than is typical of *O. rosmarus.* The curvature of the tusk exceeds that typically seen in *O. rosmarus* (cf. Rutten, 1907, Table 1). Its curvature can be matched very nearly by the right tusk of M.C.Z. 7301 (which owes its great curvature in part to extreme wear on the outer curvature), but otherwise exceeds that of any tusk in the Museum of Comparative Zoology. The initial taper of the fossil tusk is much greater than that of any Recent tusk examined.

It is of great interest to note that Leidy (1877, pp. 215-216) observed almost exactly the same dissimilarities between the tusk from the Ashley River phosphate beds and those of the modern walrus, all of which led him to suspect that his fossil represented a distinct species, which wisely he did not describe on the basis of his single example of such a variable element. Comparison between the Sarasota fossil and Leidy's description and figure [3] reveals striking similarities in gross size, curvature, taper, and fluting. The maximum anteroposterior and transverse diameters are almost identical. Leidy's specimen has a reduced transverse diameter at its proximal extremity, indicating old age and

[3] The specimen was part of a temporary exhibition of fossils belonging to the Pacific Guano Company. Recent correspondence has failed to reveal its presence in the Academy of Natural Sciences of Philadelphia or in the Charleston Museum.

cessation of growth, as is seen in old specimens of *O. rosmarus* and in *Trichecodon huxleyi* (Rutten, 1907, p. 4).

Leidy evidently did not compare his specimen with *Trichecodon huxleyi* and his paper is not cited by the subsequent writers on *Trichecodon* (van Deinse, 1943-44, Hasse, 1910, Rutten, 1907, and Lankester, 1880). Kellogg was aware of all the literature, but his paper was a review and did not deal with any of the material at first hand. These lapses may be explained in part by *Trichecodon's* having been assigned to the Tertiary, until recently, and to the very general lack of transatlantic liaison. The characters of the tusks from Sarasota and Charleston are exactly those diagnostic of *Trichecodon huxleyi*. These include robust form, great curvature, abrupt tapering, lateral compression, prominent surface and subsurface fluting, uniform transverse striation on dentinal surface, and thin cementum (Lankester, 1865, 1880; Rutten, 1907). In the aggregate, these features readily distinguish *T. huxleyi* from *O. rosmarus*, but no one character can be regarded as absolute. For example, the degree of lateral compression can be expressed in terms of the ratio of transverse to anteroposterior diameters. A series of 30 Recent tusks of *O. rosmarus* in the Museum of Comparative Zoology gives a mean ratio of .68 and a range of .59-.82. Comparable figures for eight tusks of *T. huxleyi* are .59 and .48-.71.[4] Six of the eight tusks of *T. huxleyi* have ratios of .59 or less. The Floridian and South Carolinian tusks have ratios of .61 and .59 respectively. Thus, on the basis of lateral compression alone, the American fossils fit more comfortably into *T. huxleyi* but cannot be excluded absolutely from *O. rosmarus*. That there is great variation and thus considerable overlap between species in these non-occluding teeth is not at all surprising. On the basis of all characters mentioned above, the specimens from southeastern United States may be assigned confidently to the extinct form.

PROVENANCE

The Floridian tusk was found in August, 1957, "near the edge of a marl pit in a new housing development, De Soto Lakes,

[4] The standard statistical operations were not carried out, since neither species is represented by an adequate sample. Most of the skulls of *O. rosmarus* are unsexed and without locality.

where they were digging shell for their roads. . . . De Soto Lakes is about six miles from the present shore of Sarasota Bay, and about the same distance northeast of the center of the city of Sarasota, virtually on the line between Sarasota and Manatee Counties'' (Murray, *in litt.*, April 27, 1959). According to the records and well logs of the Florida Geological Survey the Miocene Hawthorn Formation is overlain by no less than 20 feet of Pleistocene deposits in the vicinity of De Soto Lakes (Olsen, *in litt.*, June 1, 1959). Exploratory cores drilled 12 miles east northeast and 21 miles due east of De Soto Lakes reveal Pleistocene terrace sands 44 and 35 feet thick respectively (Cathcart and McGreevy, 1959, pls. 23, 24, 34). The marl is probably Pleistocene in age and represents the reworked top of the Hawthorn Formation. A sample of sand extracted from the pulp cavity of the tusk and examined by Dr. Jules R. DuBar, is considered by him to be more like the Miocene than like the Pleistocene sands of the area.

Few if any of the vertebrate fossils from the Ashley River phosphate beds bear precise locality or stratigraphic data owing to their incidental recovery in the course of commercial operations. Most of the fossil mammals are clearly of Pleistocene age, but some of the marine mammals are of probable Miocene aspect (Allen, 1926, p. 447).

The English specimens of *T. huxleyi* come primarily from a triangular area in Suffolk delimited by lines joining the towns of Ipswich, Oxford, and Walton-on-the-Naze. Most of the fossils are derived from the so-called Nodule Bed or Suffolk Bone Bed, a discontinuous, thin deposit, possibly in part reworked from older strata, at the very base of the Red Crag Series (Chatwin, 1954, pp. 42-57; Lankester, 1880, pp. 213, 216; Newton, 1891, p. 17). The Red Crag Series, formerly thought to include strata as old as Miocene, is now assigned to the earliest Pleistocene (Charlesworth, 1957, pp. 599, 1016; Chatwin, 1954, p. 42). *T. huxleyi* has also been recorded from the Cromer Forest Bed on the basis of a single tusk (Newton, 1882, p. 26; a second fragmentary tusk showed resemblances to that of *O. rosmarus*), and doubtfully from the Chillesford Beds at Aldeby on the basis of the proximal half of a femur (Newton, 1891, p. 17). The Cromer Forest Bed, which overlies the Red Crag Series, is

generally assigned to the first interglacial (Charlesworth, 1957, p. 1016; Zeuner, 1959, pp. 137-138).

The fine skull referred by Rutten to *T. huxleyi* was dredged from the sea near Breskens, West Scheldt, Zeeland, Netherlands. Rutten, influenced by the supposed Pliocene age of the Red Crag Series, attributed a Pliocene age to the Dutch fossil. The overgrowth of barnacles, perfect preservation, and considerable organic content suggest a Quaternary age for the specimen. Van Deinse (1943-1944, pp. 97-101) has subsequently reported upon two almost perfect skulls found in the same vicinity. Hooijer (1957, p. 256) has assigned these and all the "black bones" of the Scheldt estuary to the base of the Pleistocene and correlated them with the Nodule Bed of the Red Crag Series. Thus, according to current stratigraphic interpretations, *T. huxleyi* is known definitely only in the Pleistocene.[5] I am unable to determine the affinities of the fragmentary tusk from the vicinity of Antwerp inadequately described by van Beneden (1877, p. 47 and Pl. VI, fig. 8) and considered by Lankester to pertain to *T. huxleyi*.

PALEOECOLOGICAL SIGNIFICANCE

It is perhaps significant that *Trichecodon* is unknown from the cold-water members of the Crag Series, but occurs in the basal bed of the Red Crag Series, probably in the Chillesford Beds, and in the Cromer Forest Bed, all of which were laid down under temperate conditions (Zeuner, 1959, p. 143). The occurrence of *T. huxleyi* in the southeastern United States suggests that it was an inhabitant of warmer waters than is the living walrus. One hesitates to invoke boreal conditions in the surface waters of the Gulf of Mexico, as would appear to be necessary for *Odobenus rosmarus*. If such conditions prevailed, the terrestrial Pleistocene fauna of peninsular Florida, the climate of which is profoundly influenced by adjacent seas, would certainly have reflected such cooling, and it does not. It seems probable that the southerly limits of the range of *T. huxleyi* extended into warm-temperate seas.

5 Although I consider it to be unlikely, it must be admitted that the nature of the stratigraphy at the De Soto Lakes, Charleston, and East Anglian localities together with the nature of the fossils discovered at these localities (isolated tusks and a fragmentary femur only) leaves open the possibility that the fossils could be reworked from deposits as old as the Miocene. The fine Dutch material could scarcely have been redeposited.

The amphi-Atlantic distribution of *T. huxleyi* is not unexpected and is analogous to the distribution of *Halichoerus grypus* (cf. Davies, 1958, p. 110). Like the grey seal, it may never have spread into the Pacific Ocean, owing to an aversion to subarctic waters (assuming also that its range never extended far enough south to utilize the Central American water route).

With the elimination of the South Carolinian record for *Odobenus rosmarus*, the most southerly extension of the range of this species in the Pleistocene recedes northward some 230 miles to Kitty Hawk, North Carolina at 36° 03′ north (Hay, 1923, p. 29).[6] In Europe the most southerly Pleistocene localities for *O. rosmarus* are in the vicinity of Paris (Montrouge, 48° 50′ north, and Saint-Menehould, 49° 04′ north; Kellogg, 1922, p. 50). Before commenting upon these records it is necessary to discuss the Recent distribution of the walrus. Unfortunately, the walrus is firmly and erroneously associated with Arctic conditions in popular thinking and in much of the scientific literature. Allen (1930) has called attention to the fact that the walrus bred on Sable Island off Nova Scotia (44° N.) at least through 1650 and was recorded off Cape Breton as early as 1583. The number of specimens dredged from New England waters (Allen, 1930; Dow, 1954; Palmer, 1944) and a live record for Plymouth in 1734 (Allen, 1930) suggest the possibility of regular seasonal occurrence south perhaps to Cape Cod within Recent time. In Europe the walrus apparently frequented (and bred upon?) the Orkney Islands (59° N.) through 1550 (Ritchie, 1921, p. 8) and is still reported occasionally in North Sea waters (Ritchie, 1921, pp. 8, 9, 77 et sqq.; Mohr, 1952, pp. 251-254). Very little importance can be attached to the sporadic southerly occurrences of the walrus, since occasional widely extra-limital records are the rule among marine mammals. However, Sable Island and northernmost Scotland clearly did lie within the normal range of the walrus in historic time. Both Sable and Orkney Islands lie near the southern limits of the boreal sea (Clench and Turner,

6 There is in the University of Florida collections (U.F. 2112) a small fragment of the worn distal end of a walrus tusk from St. Mary's, Camden County, Georgia. Its thin cementum, outing, lateral compression, and transverse striations are suggestive of *Trichecodon*, but I regard the specimen as generically indeterminable. Dorf (1959, p. 196) states that "walrus bones have been found . . . as far as South Carolina and Georgia," which is correct only in the sense that Charleston is as far south as, indeed farther south than, much of (inland) Georgia. I am aware of no published record for the walrus in Georgia.

Ms. Zoogeographic provinces of the western Atlantic; Feyling-Hanssen, 1955, p. 25).[7] Thus, on a uniformitarian basis, a minimum hypothesis to account for the Pleistocene distribution of *O. rosmarus* would shift the southern limit of the boreal sea south to Kitty Hawk on the west and to Paris on the east. Kitty Hawk lies nearly 600 miles south of Sable Island, and Paris nearly 700 miles south of Orkney. In Recent time the range of the walrus extended 15° farther south in the western Atlantic than in the eastern. The fossil evidence indicates a figure of 13° for the Pleistocene, suggesting that similar zoogeographic zones extended farther south in the western than in the eastern Atlantic during the Pleistocene, just as they do today.

It seems likely that *T. huxleyi* ranged to the south of *O. rosmarus* on either side of the Atlantic. During glacial epochs both forms would have moved southward, with *T. huxleyi* becoming separated into American and European populations in southeastern United States (Florida and South Carolina records) and (hypothetically) southwestern Europe, while *O. rosmarus* extended its range southward to Kitty Hawk and Paris, though presumably maintaining its transatlantic connection in the north. During preglacial and interglacial epochs both forms would have moved northward, with *T. huxleyi* re-establishing transatlantic interchange between the previously isolated populations in northeastern North America (hypothetical) and northern Europe (English and Dutch records), while *O. rosmarus* retreated into high latitudes, undoubtedly establishing connection with the Pacific population at times (Davies, 1958, pp. 102-103).

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[7] It might be argued that Arctic seas extended farther south at the time when walruses occurred in these southerly localities, but they were already exterminated or nearly so by the onset of the "Little Ice Age" about 1650 (Dorf, 1959, p. 199).

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ADDENDUM

After the present paper had gone to press it was found that J. G. D. Clark (1952, Prehistoric Europe. The Economic Basis: London, Methuen & Co. Ltd., xix, XVI + 349 pp.) has noted (p. 84) the association of *Odobenus rosmarus* with prehistoric man at sites in northwestern Europe, including Skara Brae, Orkney, and Jarlshof, Shetland.

Plate 1. Medial (A) and lateral (B) aspects of tusk of *Trichecodon huxleyi*, U.F. 3274. x .4.

Plate 2. Dorsolateral aspect of proximal end of tusk of *Trichecodon huxleyi*, U.F. 3274, showing pulp cavity, globular osteodentine, and fluting and transverse striations where cementum is broken away. x1.

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CONTRIBUTIONS TOWARD A RECLASSIFICATION OF THE FORMICIDAE. III. TRIBE AMBLYOPONINI (HYMENOPTERA)

By William L. Brown, Jr.

CAMBRIDGE, MASS., U.S.A.
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Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 4 — *Contributions toward a Reclassification of the Formicidae. III. Tribe Amblyoponini (Hymenoptera)*

By William L. Brown, Jr.

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INTRODUCTION

The tribe Amblyoponini Forel as dealt with in this section has as its core the old tribe Amblyoponini of the Emery-Wheeler classification, with *Amblyopone* (including *Stigmatomma* and other synonyms), *Myopopone* and *Mystrium*. From tribe Ectatommini is transferred the genus *Prionopelta*, as already indicated in Part II of this series (see Brown, 1958a: 177, and below, under genus *Prionopelta*). *Onychomyrmex*, placed by Emery in tribe Ponerini, and by Wheeler in a separate tribe Onychomyrmicini, is here recognized as a specialized group of amblyoponines, following Clark, 1928.

In addition to these clearcut members of the tribe, there are two insufficiently known ants that may or may not belong to the Amblyoponini. One of these is *Dorylozelus mjoebergi* Forel (see below, p. 181), and the other is *Paraprionopelta minima* Kusnezov (see p. 181). These last two genera will be treated here as "*incertae sedis*" members of subfamily Ponerinae, not definitely assigned to Amblyoponini or any other tribe. However, I feel that both genera, when better known, will probably fit into existing tribes.

TRIBAL CHARACTERS

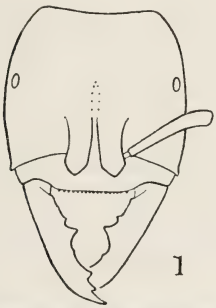
The Amblyoponini are rather homogeneous as compared to many other ant tribes. Size varies from minute (*ca.* 2 mm. total length) to medium (*ca.* 1 cm.) for workers and females, and males are within this range. The workers and females are similar in most respects, though the latter are usually larger and more heavily pigmented, with large eyes, three ocelli, and, when virgin, well-developed wings and flight sclerites in the thoracic part of the alitrunk. Females of *Onychomyrmex* form a conspicuous exception in that they are minute-eyed, wingless and otherwise "dichthadiiform." In additon, ergatoid females occur in some *Amblyopone* species, but no species is yet known to have ergatoids completely replacing normal females. The workers are essentially monomorphic, but may show wide variation in size in a single colony.

Workers and females. Amblyoponine workers have the ocelli absent (sometimes represented by one or more pits), and the compound eyes are never as well developed as in most epigaeically-foraging ant groups; typically, they are reduced to very small remnants, and they may even be absent or so shrunken as to escape ordinary microscopic observation of the integument. When they are present, the eyes are characteristically placed behind the middle of the sides of the head.

The worker-female cranium is slightly depressed (elliptical or broadly ovoid in cross section), with straight or gently convex, parallel or posteriorly converging sides. The occiput has a transverse posterior border (straight, weakly concave, or weakly convex) and broadly rounded occipital angles merging smoothly into the sides, not forming conspicuous lobes. The anterior genal

angles may or may not be toothed. Clypeus well developed, the median portion often forming a median lobe or apron and frequently with a series of teeth, tubercles or denticles along the free margin. Mandibles varying widely with genus and species, always strongly developed and inserted remotely, at the corners of the head (Figs. 1, 3, 4, 10, 15, 18, 19, 29, 30, 33-40, 48).

The labrum is broad and shield-shaped, folding back up over the smaller mouthparts when retracted, and often bearing denticles near its base, presumably to help in holding prey. The palpi are short, with segmentation ranging from 5, 3 downward, normally the same in both worker and female (with some exceptions).



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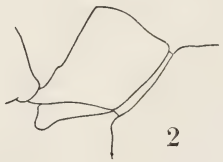


2

Amblyopone australis, worker from near Auckland, New Zealand. Figure 1. Head and mandibles, with left antennal scape, full-face view. Figure 2. Petiolar node and adjacent parts, viewed from the side.

Frontal carinae short, situated more or less near the midline, widely separated from each other or, in smaller forms, contiguous. The antennae are simple, often with a rather short, heavy scape; funiculus slender throughout to distinctly clavate at apex; the whole antenna usually has 12 segments; more rarely there are 11 segments, and in one species only 7.

Alitrunk, petiole and gaster conservative in form throughout all genera. Alitrunk long and narrow, usually more or less parallel-sided (pronotum often slightly wider) and the dorsum more or less horizontal from front to rear; promesonotal suture normally complete and possibly often mobile; metanotal groove

well-marked to obsolete. Propodeum with distinct dorsal and declivitous surfaces, rounding into each other, no propodeal teeth or angles. Metapleural glands with well-developed bulla and orifice. Petiole with little or no extended peduncle; node with steep anterior face and extensive dorsal face, but usually firmly attached to postpetiole over all or nearly all of its posterior extent, so that the dorsal face of the node is generally more or less continuous in level with the postpetiolar dorsum (Figs. 2, 31, 32, 46). This type of node is very characteristic for the tribe, and only a few scattered convergences to it exist in other ant tribes; it may well represent a structural holdover from the tiphioid wasps that gave rise to the ants. The postpetiole (abdominal III) and first gastric (IV) segments are usually subequal and ringlike, separated by a modest constriction; the succeeding segments are also ringlike, but shorter. The petiole, postpetiole and gaster together form a rather regular cylinder, usually rather long and straight (shorter in *Mystrium*). Sting present and functional.

Sculpture varying from foveolate or rugulose through reticulate-punctulate to smooth and shining. Pilosity simple, fine, varying from fairly sparse to dense, short, and pubescence-like; *Mystrium* is an exception, with many body hairs spatulate, clavate, or squamose. Color varying from blackish to pale yellow; depigmentation is common in this predominantly cryptobiotic group. Tarsal claws simple.

The known males of all genera agree in general with the description of that sex given for *Amblyopone* on page 161. The wing venation for both male and female is also covered by the variation found in *Amblyopone* (Figs. 5-7, 17, 47).

The internal anatomy of the *Amblyopone pallipes* worker and female has been studied in some detail by Whelden (1958), and the cytology by Whelden and Haskins (1954). Whelden thinks there are 9-10 Malpighian tubules in *A. pallipes,* and he covers the glandular system in some detail; the glands are apparently generally similar in kind and position to those of higher ants like *Myrmica.*

Larvae of species of *Amblyopone, Mystrium, Prionopelta* and *Onychomyrmex* have been described and figured by G. C. and J. Wheeler (1952: 113-117, 120, 637-639, 653-660), though these

authors group them according to the Emery-Wheeler classification. The larvae belong to the more primitive group among the Ponerinae, lacking tubercles over the body. Their hairs are moderately to fairly abundant and simple (denticulate or branched in most Ectatommini), though hairs are sparse or virtually lacking on the cranium in *Amblyopone*. Thoracic segments forming a slender neck in *Amblyopone;* only the first segment much narrowed in *Prionopelta;* thoracic segments broader than the first abdominal segment in *Onychomyrmex mjoebergi*. *Amblyopone* larvae are rather similar to those of *Myrmecia,* and probably approach the primitive type of larvae among ants, while *Prionopelta* is slightly and *Onychomyrmex* is more strongly specialized in the direction of the Cerapachyinae or even the Dorylinae, in agreement with their presumed nomadic existence.

Amblyoponine pupae are generally enclosed in cocoons, from which the workers can frequently emerge unaided (unlike higher ants). *A. celata* Mann apparently lacks cocoons, and the pupae are unknown for most species.

ECOLOGY AND BEHAVIOR

The members of this tribe are all, so far as known, obligatory predators of other arthropods. All or nearly all species are predominantly cryptic foragers in the soil, leaf litter or rotting logs. The nests, beyond the first stages of foundation, often tend to be diffusely spread through the substrate, and their limits may be very ill-defined and constantly shifting. One gets the impression that there is little permanent centralization of brood chambers, and that the larvae are moved about a great deal. Perhaps it is common in this tribe for the larvae to be moved to large dead prey wherever the latter is killed, rather than the reverse. I have several times found *Amblyopone pallipes* workers and larvae clustered about large lithobiid chilopods under stones in such a position as to suggest that the larvae had been transferred to the prey; Wilson (1958a) reports that *Myopopone castanea* apparently does the same thing with the large beetle larvae it preys upon in rotten logs in New Guinea. Wilson (1958b) has already proposed that behavior like that of some Amblyoponini could have led to the true army-ant foraging and nomadism, and of

course we can point to *Onychomyrmex* as an *Amblyopone*-derived stock that has already travelled a long way along this road.

Observations, some of which are reported in more detail elsewhere in this section, indicate that amblyoponine workers and nest-founding females generally attack living prey (in the form of chilopods, beetle larvae, or other arthropods), seize it in the formidable mandibles, and sting it to death with the long sting while holding on with the jaws. The prey may be much larger than the ant, and high potency is indicated for the ants' poison. The jaws, clypeus and labrum are usually toothed and well-suited to gripping active victims. The larvae feed directly on the prey when they are placed on it, or when it is given to them, and they may insert their heads into the prey's body to feed. Despite repeated trials, no one has yet succeeded in inducing *Amblyopone* workers or females to take honey, but Haskins (1928) says that *A. pallipes* will sample fruit, and that the males of this species feed avidly on honey, an interesting point in view of the importance of nectar or honeydew to tiphioids and other lower Hymenoptera, as well as to all the castes of *Myrmecia*.

Amblyopone and its relatives are moisture-loving species, most abundant in forested, temperate or tropical areas. *A. pallipes* is, for instance, often the commonest ant in wet *Rhododendron* stands in the Appalachians, and *A. australis* and several other smaller species of *Amblyopone* are common in wet, dark, fern gullies in Tasmania and southeastern Australia where most other ants are scarce. In drier areas, such as the Kansas plains or North Africa, the ants stay deep in the soil during the dry season, and are usually only found in flood times or by chance in deep man-made excavations.

Nuptial flight has been observed, at least in part, by Haskins (1928) for *A. pallipes* and by Haskins and Haskins (1951) for *A. australis*. The sum of evidence indicates that in these species, the female emerges from the nest, either flies or walks to an exposed position on rocks or foliage, and is found and mated by the male, which arrives in active flight. *A. australis* was observed "extending and arching the gaster and rubbing it with the hind legs," which suggests that it may have been releasing an attractant to draw the males. After mating, the females may return to the parent nest (*A. pallipes* always or usually; *A.*

australis sometimes) or may enter the soil or rotten wood after a time and construct a cell (*A. australis*), from which it forages actively for the prey it catches and stings to death. The cell may or may not be closed by the young female when she leaves to hunt, and prey is brought back to the cell regardless of whether brood is yet present or not. Sometimes two or more dealate females of *A. australis* apparently combine to produce a primarily polygynous nest. The most complete accounts of behavior and nest-founding are those of Haskins and Haskins (1951), and they give all the relevant earlier references. We need more information on the behavior, food and nest-founding of these and other species of Amblyoponini, because they are obviously so primitive in many ways that we may hope to learn a great deal from them about the evolution of ants in general.

RELATIONSHIPS, DISTRIBUTION AND EVOLUTION OF THE GENERA OF AMBLYOPONINI

The present record indicates that 70-75 valid species are known for the Amblyoponini of the world, of which about two thirds belong to genus *Amblyopone*. Although it is likely that more species remain to be discovered in this cryptobiotic tribe, the chances are that the proportion of *Amblyopone* species to those of other genera will increase rather than decrease. *Amblyopone* includes both generalized and specialized forms within the tribe, and it seems reasonably clear to me that all four of the remaining genera can be derived separately and directly from this large genus.

Mystrium, with 6 species in the Malagasy area, one in West Africa, and one in the Indo-Australian area, looks as though it probably arose from an African *Amblyopone* stock, although *Amblyopone* is now represented in Africa only by a very few rare species found along the western and northern fringe of the continent. *Prionopelta* is very rare in southeastern Africa and Madagascar, but is better represented in tropical America, New Guinea and the southwest Pacific islands, with outliers in New Caledonia and tropical Queensland.

Prionopelta tends to be best represented in numbers and in species where the smaller species of *Amblyopone* are rare or absent, which may indicate that *Prionopelta* has been competing

with small *Amblyopone* and winning out in some tropical areas. In similar fashion, *Myopopone castanea* may be replacing *Amblyopone australis* in a specialized rotting-log niche in Melanesia (see page 173).

Two fifths of all the *Amblyopone* species, and by far the most massive populations maintained by any members of the tribe, occur in the Australian region. Here several species, most typically *A. australis,* appear to have broken out of a small-predator adaptive zone and have secondarily enlarged in body size and become general arthropod predators. Their reduced wing venation and palpi indicate much smaller (and probably more oligophagous) ancestors, presumably much like the intergradient series of species, still existing in the Australian region, that connects them with the small "*Fulakora*" group forms. If this reasoning is correct, *A. australis* represents a case, parallel to that of *Strumigenys nidifex* Mann of Fiji, of "countercurrent evolution" (for an explanation see Brown and Wilson, 1960). The whole picture of the considerable *Amblyopone* radiation in Australia speaks of the arrival of an early stock of the genus in a practically unexploited series of niches in this isolated land mass. As we see it there today, the genus still occupies a prominent place in the cryptobiotic-predator zone in the forests of southern Australia.

One other niche left empty on the Australian continent was the army-ant niche, but this was eventually entered by an *Amblyopone* stock that developed into *Onychomyrmex* and stayed within the northern forests. *Onychomyrmex* is now probably in competition with two or three species of the army-ant genus *Aenictus* Shuckard that appear to have extended their ranges into tropical Australia from the north in recent times.

Other relatively weak relictual representations of *Amblyopone* occur in the Americas, especially in temperate North America and southern South America, in New Zealand, in the Mediterranean area, in southern and eastern Asia, and in the East Indies. A single small species in Hawaii may have been introduced by man. But the presence of undoubted endemic members of the tribe in extralimital regions like Chile, New Zealand, New Caledonia, southwestern Australia, Tasmania, Cuba, Japan, Madagascar and the Solomons, speaks for an old, worldwide distribution. Tribe Amblyoponini apparently is the surviving remnant

of a much larger and more varied group of ants, probably dating back to the Cretaceous. Today, the tribe is reduced to the few stocks that survived contact with more progressive ant groups only because they became specialized for relatively constant, predominantly cryptobiotic niches. Even though they thus managed to avoid the heaviest competition, the general scarcity of amblyoponines outside a few limited and usually more or less peripheral areas points to their decline as a world group.

Unfortunately, we have no fossil record of the tribe, although the morphology, habits and distribution indicate a greater age than for the Ectatommini, which were present and widespread in the Oligocene. The petiolar-gastric structure may indicate direct lineage from the proto-formicid stem, but in other characters (including loss of anal lobe in hind wing, reduction of palpi and eyes, elaboration of mandibles, simple tarsal claws, and 6-partite proventriculus) the tribe is specialized.

TREATMENT OF SPECIES-LEVEL TAXONOMY

As already stated in Part II of this series, the primary aim of the work is a revision of classification at the generic level. But in the course of such work there is always uncovered a mass of information concerning new synonymy, undescribed forms, geographical variation, biology, etc., at the species level, which logically should go with a survey of this kind. As in Part II, such information has been placed in the Appendix, where the items are listed consecutively against boldface numbers in brackets corresponding to the bracketed numbers in the text.

Former varieties and subspecies have been eliminated as such in the species lists, and are either synonymized or treated as species. Revisionary studies at species level were carried to completion only in the cases where a clearcut decision seemed possible on the basis of the available material. In a few other cases, the taxonomic problems involved have been discussed, but not settled. It is obvious that more work needs to be done at the species level, particularly in *Prionopelta,* in the Madagascan *Mystrium,* and among the Far Eastern *Amblyopone.* In the case of the few names arbitrarily raised from infraspecific to specific rank, this action does not necessarily carry any implication of support for their distinctness as species.

The capital letters placed in parentheses before each specific name indicate the kind of evidence upon which the present generic placement is directly based.

(T) indicates that type material, nidotypes, reliably type-compared material, or similarly authentic specimens have been examined, in most cases by myself; rarely, examination has been made by other myrmecologists.

(P) means that material identified from reasonably good descriptions, or from other satisfactory evidence, has been examined and is thought to be correctly determined.

In cases where the species is not seriously questioned, but no specimens referable to it have been seen, or if specimens seen cannot be satisfactorily verified as to identity, no entry has been made before the species name.

(?) signifies that, in my opinion, the species is inadequately described for purposes of distinction and that its taxonomic status is doubtful.

The species lists have been based on various myrmecological compendia and basic papers, and were checked against Emery's Genera Insectorum list and the Zoological Record, 1908 through 1955. References through 1958 are included so far as I am aware of them. I shall consider it a great favor if readers will send me notice of the inevitable omissions for inclusion in a corrective supplement.

Key to the Genera of Amblyoponini, based on the workers and females

1. Mandibles short, narrow, closing tightly against the clypeus, their apical borders distinct and completely occupied by 3 large teeth, of which the middle tooth is shortest; basal border of mandible unarmed (Fig. 15; widespread in tropics) ..... *Prionopelta* Mayr[1]
   Mandibles of another form, usually strongly projecting beyond clypeus when closed, and with more than 3 teeth (Figs. 19, 29, 48) ..... 2.

2. Antennal funiculi markedly compressed; when head is viewed in perfect full-face view, lobes of frontal carinae are approximately even with, or slightly surpass, the anterior clypeal border beneath them (Fig. 10; Indo-Melanesian area, widespread) ..... *Myopopone* Roger

[1] *Dorylozelus* Forel, of Queensland, may be an amblyoponine, in which case it would key out to *Prionopelta*.

Antennal funiculi not compressed, approximately round in cross section; in full-face view of head, lobes of frontal carinae distinctly behind the anterior median clypeal border (Figs. 19, 29, 40) ..... 3.

3. Apex of mandible bluntly rounded or subtruncate as seen from above, although the inner apical margin may bear two or more small teeth, triangular in shape and often retrorse; many body hairs clavate or spatulate (Fig. 4; Madagascar, w. Africa, Indo-Australian area)

Mystrium Roger

Apex of mandible in the form of an acute tooth (Figs. 19, 29, 30, 33, 40, 48); body hairs simple, fine and tapered ..... 4.

4. Tibia of posterior leg without an apical spur, or at most with a very small, straight, non-pectinate vestigial spur; small, slender, predominantly smooth and shining species with greatly enlarged tarsal claws on middle and posterior legs; queens wingless, small-eyed (''dichthadiiform''); probably with legionary habits (Figs. 46-48; Queensland)

Onychomyrmex Emery

Tibia of posterior leg with a well-developed apical spur having a curved, broadly pectinate inner margin; species of diverse size and form, with tarsal claws rarely enlarged; in cases where they are enlarged, the head and alitrunk tend to be coarsely sculptured and often opaque; virgin queens normally winged and with large compound eyes (Figs. 29, 33, 40; widespread in temperate and tropical areas, but often local; not known from e. and s. Africa or Madagascar) ..... *Amblyopone* Erichson

THE GENERA

Amblyopone Erichson

> *Amblyopone* Erichson, 1842, Arch. Naturg., 8(1): 260. Type: *Amblyopone australis* Erichson, 1842, monobasic.

> *Stigmatomma* Roger, 1859: 250. Type: *Stigmatomma denticulatum* Roger, 1859, by designation of Bingham, 1903. N. syn.

> *Arotropus* Provancher, 1881, Naturaliste Canad., 12: 205. Type: *Arotropus binodosus* Provancher, 1881, monobasic.

> *Stigmatomma* subgenus *Xymmer* Santschi, 1914: 311. Type: *Stigmatomma* (*Xymmer*) *muticum* Santschi, 1914, monobasic.

> *Stigmatomma* subgenus *Fulakora* Mann, 1919: 279. Type: *Stigmatomma* (*Fulakora*) *celata* Mann, 1919, by original designation.

> *Amblyopone* subgenus *Neoamblyopone* Clark, in Wheeler, 1927: 1. Type: *Amblyopone* (*Neoamblyopone*) *clarki* Wheeler, 1927, by original designation, monobasic.

> *Amblyopone* subgenus *Protamblyopone* Clark, in Wheeler, 1927: 1. Type: *Amblyopone* (*Protamblyopone*) *aberrans* Wheeler, 1927, by original designation, monobasic.

> *Lithomyrmex* Clark, 1928: 30. Type: *Lithomyrmex glauerti* Clark, 1928, by original designation, monobasic. N. syn.

> *Ericapelta* Kusnezov, 1955: 273. Type: *Ericapelta egregia* Kusnezov, 1955, monobasic. N. syn.

(For previous writings on synonymy and relationships of *Amblyopone* at generic and subgeneric level, see Wheeler, 1927; Clark, 1928; Brown, 1949).

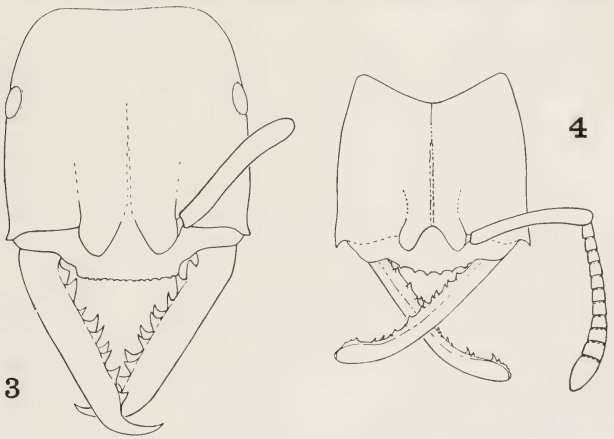
Amblyopone is a curious genus containing a large and heterogeneous array of species, which represents the residue left after dividing a few specialized amblyoponines among the few other genera recognized here. *Amblyopone* is not only residual as a genus; it is "central," which is to say that it is probably to be regarded as the stock from which the other genera have risen. While its species differ widely in size, color, sculpture and in the structure of the cranium, clypeus and mandibles, the general form of the remainder of the body is remarkably uniform in nearly all of them. In fact, departures such as the pedunculate petiole of *A. mutica* are slight when compared to the variation among species of other genera of ants, and stand out in *Amblyopone* only because the great majority of species in the genus are so monotonously similar in posteephalic body form.

The most characteristic trait of *Amblyopone* (and most other Amblyoponini), aside from general habitus, is the structure of the petiole and its mode of attachment to the postpetiole (Figs. 2, 31, 32). The petiole is nodiform and robust, with an abruptly descending anterior face to the node and an approximately horizontal dorsal face. No true posterior face is differentiated, the node attaching directly, with little or no posterior constriction, to the postpetiole. There is usually an anteroventral process adorning the petiolar keel. The postpetiole is functionally a part of the gaster, and is large, with only a moderate constriction between it and the structurally similar succeeding segment (IV abdominal). In both the postpetiole and the IV abdominal segment, the tergites are immovably fused to the sternites.

These characters of the petiole and gaster are shared by all castes, including the males, and they are also more or less faithfully copied by all of the other genera of the tribe. The conformation of this region appears to be of a very primitive kind among the ants, and is similar to that seen among scolioid (tiphioid) wasps. This group of wasps is primitive among the

aculeate Hymenoptera, and probably included, sometime during the Cretaceous, the ancestral stem of the Formicidae. The sting in worker and female *Amblyopone* is long, sharp, heavily sclerotized and obviously functional.

In the female and worker *Amblyopone* there is a fundamental uniformity in the structure of the head and mandibles despite the great interspecific differences one finds in detail. The mandibles always end in an acute (usually dentiform or spiniform) apex, and the eyes, when present, are situated behind the middle



Heads of amblyoponine workers, full-face view. Figure 3. *Amblyopone* sp. of *reclinata* group from Macao. Figure 4. *Mystrium camillae* from near Darwin, northern Australia.

of the sides of the head. The clypeus forms a band across the anterior part of the head, and its median portion is usually more or less projecting to form a low, broad lobe or apron, which in most but not all species bears a row of denticles or small tubercles.

The mandibles are linear (rarely triangular) and inserted far apart at the corners of the clypeus; when at rest, their apical portions cross over one another. In most species, the basal border

is absent or very poorly developed, and the masticatory margin may either include it or be formed entirely of the apical border. The dentition consists of few (more than 3) to many teeth, varying in size and form, and ranked in one or two rows along the masticatory border (Figs. 1, 18, 19, 29, 30, 33-40). The dentition, of course, varies widely according to species, and some species show considerable intraspecific variation also. Fundamental generic characters are the presence of more than three teeth and the more or less acute nature of the apex.

Most, but not all, species of *Amblyopone* bear on each anterolateral angle of the head a more or less distinct and usually acute, dentiform extension of the gena (Figs. 3, 33, 40) which I have previously called the "amblyoponine tooth." However, the term "genal tooth" used by Wilson (1958a) is more specific and objective, and I feel should be preferred.

The frontal carinae form narrow lobes in front; the carinae and lobes may be widely separated (Fig. 29), close together or even fused (Fig. 40), fusion or close proximity usually being correlated with extreme reduction of size, depigmentation and other traits of specialized subterranean life forms. The lobes reach or overlap the clypeus in front, but do not surpass the anterior border of the median lobe or apron (Figs. 29, 40).

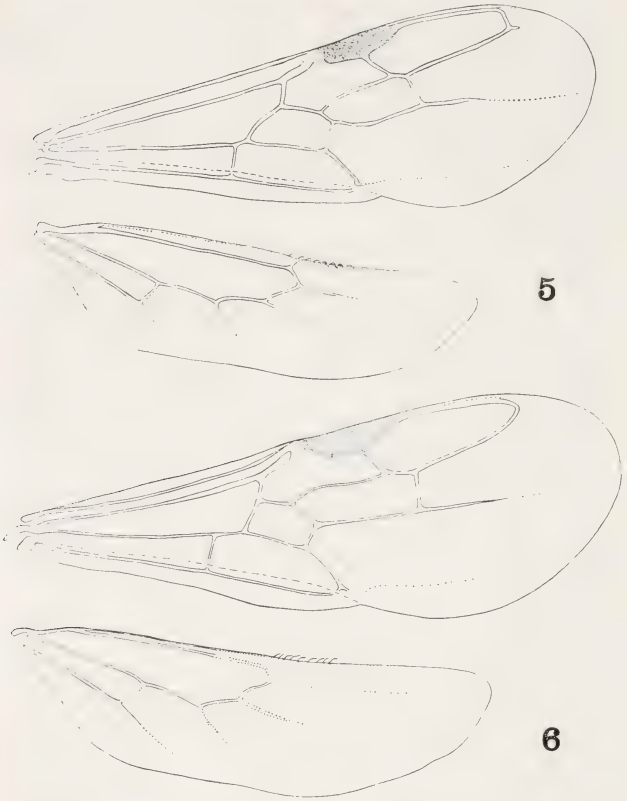
The antennae are usually 12-segmented in the female castes, but in one species, *A. degenerata* Borgmeier, fusion has reduced the number to only 7 distinct segments. The flagellum varies from slightly incrassate toward the tip to distinctly clavate, according to species.

The labium is a broad, tongue-shaped flap or shield, apically more or less deeply emarginate, hinged at the base so as to be able to cover the smaller mouth-parts when in repose, or to swing forward under and between the mandibles to assist in holding prey or perhaps other objects as well. The maxillary and labial palpi are always more or less reduced, as usual in ants with hypogaeic tendencies; there is wide variation in the number of segments among the different species, and some variation has also been noticed within certain species. The highest counts noted are those of *A. impressifrons* (5 maxillary, 3 labial) and the *reclinata* group (5, 3 or 4, 3), and several species are known to have counts of 4, 3, or 3, 2, or 2, 2; a female of *A. saundersi* from

New Zealand had maxillary 1, labial 2, although a worker assigned to the same species had 2 and 2.

The alitrunk is elongate, more or less parallel-sided, with a distinct and complete promesonotal suture, in most species apparently representing a flexible joint separating the two main parts of the alitrunk. Metanotal groove present and distinct in most larger forms, but lost or obsolescent in most smaller species. Mesonotum (when fully distinguishable) short and transverse. Propodeum unarmed, bluntly rounded into declivity. Sting long and stiff, fully functional.

Female like worker, and usually only slightly larger in size, with large compound eyes, ocelli well developed, and flight sclerites differentiated; however, the alitrunk is low and has a relatively straight profile. Wings present; venation varying widely with the species, and often within species, but relatively complete even in the smaller species. Some of the larger or medium-sized species have all of the "primitive" ant venation in both wings, except for the first radial crossvein, which is present only as an occasional atavism (Brown and Nutting, 1950:125). In many of the smaller species, as well as in the large *A. australis* and some of its large and medium-sized relatives, the forewing has lost Rsf2+3 partly or entirely (compare Figures 5 and 6 with Figure 7). Venation is particularly variable in *A. australis* (of both sexes), and this appears to be the normal situation, not just due to "abnormality" as suggested by Kusnezov (1955:268). In this species, Rsf2+3 may be completely absent, present as a spur of varying length in its apical portion, or, more rarely, present only as a variable free section attached to an atavistic first radial crossvein; Mr. John Clark long ago sent me many sketches of forewings of this last type. The anal vein varies in development with the species, and may extend to or very nearly to CuA (thus closing a "second discoidal" cell), or may fall short by a greater or lesser distance. The "open" or "closed" condition of "cubital" or "discoidal" cells, upon which Kusnezov so largely based his 1955 classification, is in my opinion a virtually useless character-system because of the wide variation and subtlety of the occurrence of the veins themselves, among species as well as within certain single species. I should like to re-emphasize the position taken in 1950 by Brown and Nutting: the



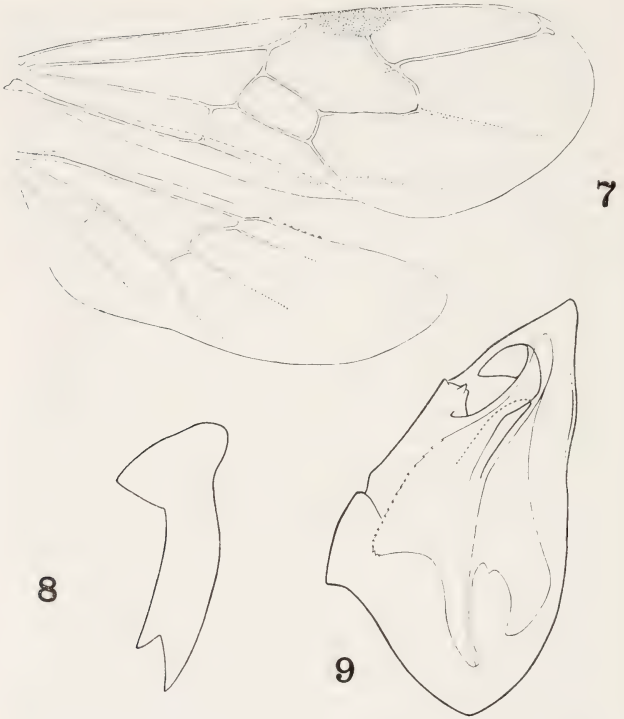
Wings of males of the *reclinata* group, species indeterminate. Figure 5. Specimen from Los Baños, Luzon, (terminalia shown in Figs. 22, 24, 27). Figure 6. Specimen from Chipon, Formosa (terminalia shown in Figs. 23, 25, 28).

most attention should be paid to the veins themselves; descriptions of "cells" in ant wings convey much less information, and convey it less precisely. In the *Amblyopone* species so far checked, the hind wing always lacks an anal lobe.

The sculpture of worker and female is much alike in general, but varies according to species and species-groups. The head, and to a lesser extent the alitrunk, is usually much more distinctly sculptured than the gaster; frequently the gaster is predominantly smooth and shining, with scattered fine punctulae. The sculpture of the head varies from smooth and shining, with or without some foveolae or costulae, through coarse or fine striation (in most cases predominantly longitudinal), subvermiculate rugulation, to fine, dense, reticulopunctation or reticulo-striolation. The mandibles may be striate, punctate or smooth. The posterior sides of the alitrunk, especially near the metapleural glands, are frequently superficially striate, a feature that may be connected with distribution of material from the glands. Pilosity is simple and fine, and ranges from short, dense, pubescence-like pile to longer and sparser hairs of irregular length.

The male of *Amblyopone* is normally smaller and more slender than the corresponding female, and has an entirely different head, usually or always broader than long, including the large, convex compound eyes. The mandibles are slender, curved, strap-like, the apex simple and acute or with two coarse teeth; when closed, their tips meet or overlap, and the entire blades are usually tucked away (rarely not) under the clypeus in such a way that only their external margins show externally along the anterior clypeal border. Clypeus usually convex and most often with a rounded anterior border or apron that frequently carries serially-arranged denticles or tubercles homologous to those of worker and female, where they are present in these castes. Anterior border more rarely transverse and approximately straight.

The male antennae are slender, but often slightly to moderately incrassate toward their apices; the scape is short, but usually more or less slender-cylindrical; funiculus 12-segmented in all of the species for which the male is known, but could conceivably be of a smaller count in unknown males of species like *A. degenerata* (see under *Paraprionopelta*, below). The funicular segments increase in length toward the tip, the apical segment being the longest one.



Amblyopone australis, male taken with workers at Dorrigo, New South Wales. Figure 7. Wings. Figure 8. Mandible dissected out of head. Figure 9. Left half of genitalia as viewed from midline; valve of aedeagus drawn as a very light line.

The under-mouthparts are in many ways similar to those of the corresponding workers and females, and frequently the palpi have the same segmental counts as the workers (2, 2 to 5, 3, of course varying with the species). In *Amblyopone australis,* however, the male has a formula of 4, 3, while the worker

has only 2 and 2. A similar situation probably holds in some of the other species, particularly those related most closely to *A. australis*. The formula of the male may therefore be said to be either like that of the corresponding worker, or else more conservative.

Alitrunk with well (but not excessively) developed flight sclerites; notauli present and distinct, usually forming a complete Y. Propodeum unarmed. Petiolar node in general shape as in worker-female, but may be more slender or differ otherwise in proportions; a ventral lobe or process is usually present anteriorly. Petiolar attachment and general form of anterior gaster much as in worker; posterior portion modified, of course, to receive genitalia. The VIII, and often the VII, sternites are broadly emarginate posteriorly. The subgenital plate (or hypopygium, sternite IX) varies greatly with the species; sometimes it is rather simply tongue-shaped, but it is highly modified in some species, and may even (some species of *reclinata* group) possess a more or less well developed slender median caudal process (Fig. 23). The pygostyles are usually present, but occasionally are absent, or at least so reduced that they were not noticed in the dissections. The phallus is constructed on the usual formicid plan, but there is a great deal of modification of the particular components in many of the species, so that the genitalia in this group furnish much better species characters than is usual in ants. A few of the variations are illustrated in Figures 9, 24, 25, 27, 28 and discussed in [8]. The genitalia are, however, not very useful in distinguishing *Amblyopone* from other genera of the tribe, because the intrageneric variation is much greater than the intergeneric.

Males tend to be blackish in general color, or at least darker than the corresponding workers, but some of the forms from Old World desert areas are lighter, more brownish or even yellowish in color. Probably many of the males are nocturnal, so that more species will be found to be light in color. Male sculpture often follows in a rough way that of the workers of the same species, but tends to be much better developed and coarser over the head and alitrunk, though often less regular and more rugose or vermiculate.

In general size, the species of *Amblyopone* vary considerably, the smallest workers (*A. degenerata*) being in the neighborhood of 2 mm. outstretched length, while large workers and females of *A. australis* are robust insects, reaching a centimeter and more in length. Some of the species are very variable in size in the worker caste, but polymorphism is not well developed even in these. Allometric differences affect mostly things like proportions (width) of head and petiole, and size of eyes.

The synonymy of *Amblyopone* and *Stigmatomma* was discussed in detail, and previous references to the subject mentioned, in Brown, 1949: 86; see also Brown and Nutting, 1950: 124. In the 1949 paper, *Stigmatomma* was reduced once again to subgeneric status under *Amblyopone*. *Xymmer* and *Fulakora* were synonymized with *Stigmatomma*. *Stigmatomma* had previously been separated on the basis of its "double-ranked" (vs. "single-ranked" in *Amblyopone*) mandibular dentition; its finer, more opaque cephalic sculpture; and the supposed absence of teeth on the anterior clypeal border of *Amblyopone*. But, as is now fairly widely appreciated by myrmecologists, the double-ranked condition grades through, especially in some Australian species of the *ferruginea* group. Most of the "true" *Amblyopone* as formerly separated have denticulate anterior clypeal borders, although this denticulation is often very fine, and may occasionally be absent, as explained below. The sculptural distinction is worthless, since some species with *Stigmatomma* characters otherwise, e.g. *A. normandi*, *A. elongata*, have the dorsal surface of the head predominantly smooth and shining. On the other hand, some *Amblyopone s. str.* have densely sculptured heads (e.g., *ferruginea* group). There remains the question of the presence or absence of Rsf2+3 (which determines whether there are one or two cubital cells). In 1949, I maintained this as a provisional separatory character at the subgeneric level, stating at the same time my doubts as to its usefulness when more material became available. Now that we have more material of the winged castes of various species, it is clear that Rsf2+3 has been lost independently at least twice, and possibly more than three times, that is, in the Australian "true" *Amblyopone* (where variable remnants of Rsf2+3 are common), in a South American species (the "*Ericapelta egregia*" of Kusnezov), and in certain of the smaller

species (e.g., *A. saundersi* of New Zealand). A generic split along these lines would certainly be discordant with divisions that might possibly be drawn on the basis of other characters, and as a matter of fact, it turns out that some species that would be placed in *Amblyopone* on the basis of venational characters have workers that would go into *Stigmatomma*. The *Amblyopone-Stigmatomma* dichotomy certainly loses its former supposed sharpness, and I see no reason to maintain a separate formal subgenus for *Stigmatomma* any longer.

The subgenus *Xymmer*, based on the sole West African species *Stigmatomma* (*Xymmer*) *muticum* Santschi, has a median clypeal apron absolutely devoid of teeth along its anterior margin, but in 1949 I synonymized this subgenus with *Stigmatomma* because of the similar condition reported by Forel for *S. bellii* of southeastern Asia. However, the types of *S. bellii* have been examined again, and they have been found to possess denticulation of the clypeal apron, although the denticles are small and rather indistinct. Since *muticum* also has the petiole conspicuously narrowed into a slender, short peduncle at its base, a case might be made for the resurrection of *Xymmer* as a generic or subgeneric name for this aberrant species. However, we now know at least one more species, *A. gingivalis* sp. nov., that definitely lacks teeth or denticles on the clypeal margin; *gingivalis* is aberrant in the form of its mandibles, but the petiole is normal for the genus. Several species, especially *A. bruni*, have clypeal denticulation reduced very nearly to the vanishing point. I have examined types of *S.* (*X.*) *muticum*, and in the light of what we now know about variation among *Amblyopone* species, I believe that this species should be included in the genus without subgeneric distinction. (In practice, I have found formal subgenera to be awkward and confusing, and I much prefer to use informal species-groups that do not clutter the nomenclature.) Actually, *A. mercovichi* and *A. gingivalis* are more aberrant in some respects than is *A. mutica*, to say nothing of *A. degenerata*, which Borgmeier wisely placed in *Amblyopone* when he first described it.

Clark has suggested (*in litt.*, 1948) that *A. reclinata*, *A. rothneyi* and allies with more or less large compound eyes should be segregated in a separate genus, but here again there seems

to be much variation leading toward more "normal" kinds of *Amblyopone,* of which perhaps *A. pallipes* or *A. silvestrii* would represent an average species. Probably further investigation will only strengthen the links between this group and the rest of the *Amblyopone* species.

Lithomyrmex is another generic name proposed for a single species, *glauerti* Clark from Western Australia. This species, as Clark suggests, may indeed represent an intermediate form leading from *Amblyopone* to *Onychomyrmex,* but the females are normal (winged as virgins), and the three castes cannot be separated from the corresponding ones of *Amblyopone* by any really important character. As an *Amblyopone, glauerti* cannot even be considered as more than a moderately aberrant species.

The species of *Amblyopone* are found in many countries widely scattered over the earth, ranging from tropical to cool temperate in climate, and from wet to rather arid. The Australian Region, with about two-fifths of the known species, is the headquarters of the genus. Another fifth of the species is found in tropical Asia, and still another fifth is distributed through the Americas, from Canada to Chile. The remainder of the species are scattered; several are in the Mediterranean area, two are on the western fringe of Africa in Nigeria and Senegal, one is in Japan, and one, possibly introduced from Melanesia, is in Hawaii. The concentration of species in extralimital regions such as Chile, Argentina, Cuba, Japan, Australia, the Solomons and New Zealand speaks for the age of the genus. Its absence or great rarity in the central Ethiopian Region is parallel to that of other ancient groups, such as tribe Ectatommini and the "*Notomyrmex*" group of *Monomorium,* that are well developed in the peripheral areas listed above with *Amblyopone.* Unlike the more open-foraging ectatommines, however, the amblyoponines are not represented in Tertiary fossil faunas, indicating that even during those periods, *Amblyopone* did not include prominently arboreal foragers, at least in the Northern Hemisphere.

This leads us again to the obvious observation that *Amblyopone* species are mostly small and hypogaeic specialists, although it should be noted that some of the members of the tropical Oriental *reclinata* group are fairly large in size, are heavily

pigmented, and have fairly large eyes in the worker caste, like workers of some known epigaeic foragers in other tribes of ants. However, we have no direct information on the habits of any member of the *reclinata* group, and it seems unlikely that species of this group are strongly epigaeic in foraging habits.

Most species of *Amblyopone* so far known have been found in moist, forested areas, where they may nest in rotten wood, in the leaf litter, or in the soil under stones or logs. Nevertheless, several species are known to be tolerant of rather arid conditions in treeless regions in Australia, North America, Argentina, North Africa and the Middle East, where the subterranean habits are strongly developed, and some species are known only from males taken at light **[1, 12]**.

So far as my reading and experience go, the *Amblyopone* species feed nearly or quite exclusively on arthropods, dead or alive at time of interception. *A. pallipes*, and probably other species, specialize on chilopods **[2, 16]**. *A. australis*, judging from remains in the nests, collects various arthropods, including beetles.

Amblyopone Species

(T) *aberrans* Wheeler, 1927:26. W. Australia [**16**, Fig. 35]
amblyops Karawajew, 1935:57. N. comb. Indo-China [**11**]
(P) *armigera* Mayr, 1887:547. se. Brazil, n. Arg. [**1**]
(P) *australis* Erichson, 1842, Arch. Naturg., 8(1):261 [**13**, Figs. 1, 2, 7-9]
(P) = *obscura* Fr. Smith, 1858, Cat. Hym. Brit. Mus., 6:109.
(P) = *cephalotes* Fr. Smith, 1876, Trans. Ent. Soc. Lond., p. 490.
(T) = *laevidens* Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, 25:447.
(T) = *fortis* Forel, 1910:1.
(P) = *maculata* Stitz, 1911, Sitzb. Ges. Naturf. Freunde, Berlin, p. 351.
(P) = *nana* Emery, 1914, Nova Caledonia, Zool., 1:394.
(T) = *minor* Forel, 1915:1.
(T) = *foveolata* Wheeler, 1927:9.
(T) = *pallens* Wheeler, 1927:11.
(T) = *queenslandica* Wheeler, 1927:12.
(T) = *norfolkensis* Wheeler, 1927:15.
(T) = *howensis* Wheeler, 1927:15.
(T) *bellii* Forel, 1900:55. India [**8**]
bierigi (Santschi), 1930, Bull. Soc. R. Ent. Egypte, (n. s.) 14:17. Cuba [**7**]
(P) *bruni* (Forel), 1912, Ent. Mitt., 1:45. Formosa [**9**, Fig. 21]

(T) = *juergi* (Forel), 1922, Rev. Suisse Zool., 30:87. N. syn.
(T) *eclata* (Mann), 1919:279. Solomon Is. [18]
(P) *chilensis* Mayr, 1887:547. Chile [1]
(T) *clarki* Wheeler, 1927:24. sw. Australia [16, Figs. 33, 37, 38]
(T) *degenerata* Borgmeier, 1957:111. se. Brazil [7]
(P) *denticulata* (Roger), 1859:251. N. comb. s. Europe [12]
= *gheorghieffi* Forel, 1892, Verh. zool.-bot. Ges. Wien, 42:309. Syn. by Emery, 1916:100.
(P) =*gracilicornis* (Menozzi), 1936, Boll. Lab. Zool. Portici, 29:268. N. syn.
(P) *elongata* (Santschi), 1912:519. se. Brazil to n. Arg. [1]
= *barretoi* (Bruch), 1921, Rev. Mus. La Plata, 26:184. Syn. Borgmeier, 1957.
= *minor* (Santschi), 1922, An. Soc. Cient. Arg., 94:241, *nec* Forel, 1915. Syn. Borgmeier, 1957.
(P) = *parancnsis* (Santschi), 1924, Ann. Soc. Ent. Belg., 64:6. Syn. Borgmeier, 1957.
(T) *egregia* (Kusnezov), 1955:274. N. comb. n. Argentina [1]
(T) *emeryi* (Saunders), 1890, Ent. Mon. Mag., 26:203. N. comb. n. Africa [12]
(P) *exigua* Clark, 1928:35. Australia: Victoria [17, Fig. 44]
feai (Emery), 1894, Ann. Mus. Civ. Stor. Nat. Genova, 34:454. Burma [8]
(T) *ferruginea* Fr. Smith, 1858, Cat. Hym. Brit. Mus., 6:110. Australia: vic. Melbourne [16, Fig. 36]
(T) = *mandibularis* Clark, 1928:33. Syn. Brown, 1952.
(T) *gingivalis* Brown, sp. nov. e. N. S. Wales [15, Figs. 30, 31]
(T) *glauerti* (Clark), 1928:31. N. comb. W. Australia
(T) *gracilis* Clark, 1934b:52. Australia: Victoria [16, Fig. 41]
(T) *hackeri* Wheeler, 1927:22. se. Queensland [16, Fig. 39]
(P) *impressifrons* (Emery), 1869, Ann. Accad. Aspir. Natural., Napoli, (2)2:13. Italy [12]
(T) *leai* Wheeler, 1927:16. Lord Howe I. [13]
(T) *longidens* Forel, 1910:1. se. Australia [16, Fig. 34]
(T) *lucida* Clark, 1934a:27. Australia: Capital Terr. [17, Fig. 45]
(T) *luzonica* (Wheeler & Chapman), 1925:56. N. comb. Philippines [11]
(T) = *williamsi* (Wheeler & Chapman), 1925:56. N. syn.
(T) *mercovichi* Brown, sp. nov. se. Australia [14, Figs. 29, 32]
(P) *michaelseni* Forel, 1907, Fauna SW Australia, 1:264. sw., se. Australia [13]
(T) *minuta* (Forel), 1913, Zool. Jahrb. Syst., 36:4. E. Indies [10]
(T) *monrosi* Brown, sp. nov. Chile [5]
(T) *mutica* (Santschi), 1914:311. N. comb. Nigeria

(T) *mystriops* Brown, sp. nov. Guatemala [**4**, Fig. 19]
(T) *normandi* (Santschi), 1915:54. N. comb. Tunisia [**12**]
(T) *oregonensis* (Wheeler), 1915:389. n. California to Brit. Columbia. N. status [**2**]
(T) *orizabana* Brown, sp. nov. Mexico: Mt. Orizaba [**6**]
(P) *pallipes* (Haldeman), 1844, Proc. Acad. Nat. Sci. Philadelphia, 2:54. s. Quebec and Iowa to Florida and Arizona [**2**]
[= *serrata* (Roger), *Arotropus binodosus* Provancher, *arizonensis* (Wheeler), *wheeleri* (Santschi), *montigena* (Creighton). Synonymy in Creighton, 1940; Brown, 1949:84.]
(T) = *subterranea* (Creighton), 1940:8. N. syn.
(P) *punctulata* Clark, 1934a:28. Tasmania [**17**]
(?) *quadrata* (Karawajew), 1935:57. N. comb. Gulf of Siam [**8**]
(P) *reclinata* Mayr, 1878, Verh. zool.-bot. Ges. Wien, 28:667. Java [**8**]
(T) *rothneyi* Forel, 1900:56. India: Bengal [**8**]
santschii (Menozzi), 1922, Ann. Mus. Civ. Stor. Nat. Genova, 49:347. N. comb. Senegal [**12**]
(T) *saundersi* Forel, 1892, Mitt. schweiz. ent. Ges., 8:336. N. Zealand [**17**]
(T) *silvestrii* (Wheeler), 1928, Boll. Lab. Zool. Portici, 21:97. Japan [**11**]
(T) *smithi* Brown, sp. nov. S. Australia: Lofty Range [**17**, Fig. 40]
(T) *trigonignatha* Brown, 1949:81. N. Carolina [**3**, Fig. 18]
wilsoni Clark, 1928:34. se. Australia [**17**]
zwaluwenburgi (Williams), 1946, Proc. Hawaii. Ent. Soc., 12:639. N. comb. Hawaii: Oahu [**19**]

Mystrium Roger

= *Mystrium* Roger, 1862:245. Type: *Mystrium mysticum* Roger, 1862, monobasic (+7 spp.).
= *Mystrium*, Wheeler, 1922:758, 1006, synonymic catalog of African and Malagasy spp.
= *Mystrium*, Menozzi, 1929:518-536, revision of the genus.

This most aberrant genus is close to *Amblyopone*. The workers and females differ from those of *Amblyopone* in their shorter, thicker bodies and broader heads, as well as their odd, blunt-tipped mandibles (Fig. 4). The sculpture is rather coarse and consists of bold reticulation or costulation over head and much of alitrunk. Within the reticular basins and elsewhere are situated the peculiar body hairs, which are generally squamose-pointed, clavate, or otherwise broadened or bizarre. Menozzi notes that the worker-female palpal formula is 4, 3, a count that I have confirmed for an *M. rogeri* worker in the Museum of Comparative Zoology.

Male like that of *Amblyopone*, coarsely sculptured and with notauli distinct. Wing venation of both sexes of the "complete" type (Fig. 5).

Genitalia not studied. Pygostyles apparently lacking.

So far as known, *Mystrium* is limited in distribution to Madagascar and adjacent islands (six nominal species), Cameroons (one species), and the Indo-Australian area, where one species *M. camillae*, has been found in Burma, the East Indies, Luzon, New Guinea and the Darwin district of northern Australia. It is assumed that *Mystrium* is predaceous, but there is no direct evidence known to me on its feeding habits. Almost equally scanty is information on colony size, nest site and structure, and most aspects of ecology and behavior.

Menozzi's revision (1929) includes a key to the species, plus illustrations and descriptions. It is difficult to judge the status of the species from Madagascar, since most of these are known from inadequate material. Since Menozzi gives full references to all species, only the dates of description are given in the list below.

Mystrium Species

(P) *camillae* Emery, 1889. Burma to n. Australia. [Fig. 4]
(P) = *javana* Karawajew, 1925. N. syn.
fallax Forel, 1897. Madagascar: Nossi Be.
(P) *mysticum* Roger, 1862. Madagascar, Comoro Is.
(T) *oberthueri* Forel, 1897. Madagascar.
(T) *rogeri* Forel, 1899. Madagascar.
silvestrii Santschi, 1914. Cameroons.
stadelmanni Forel, 1895. Madagascar.
(T) *voeltzkowi* Forel, 1897. Madagascar: Nossi Be.

Myopopone Roger

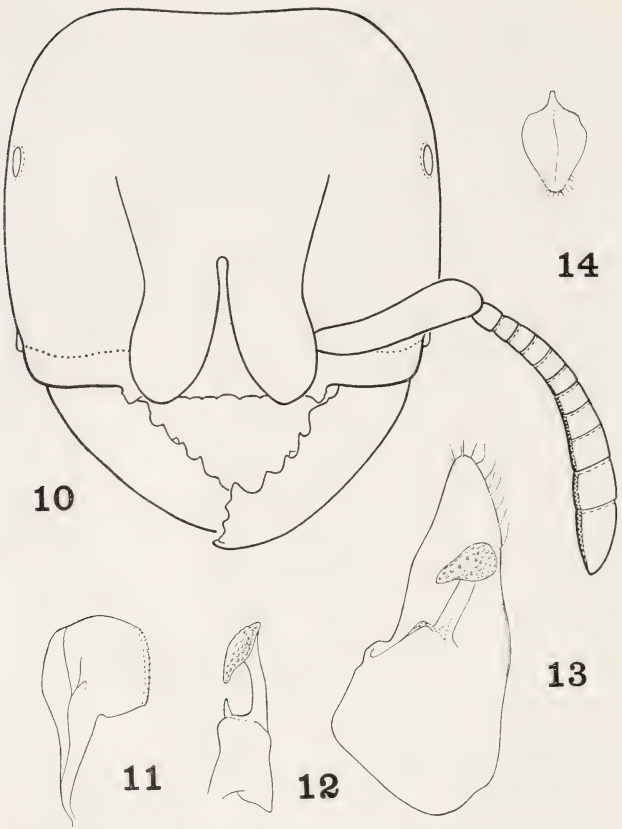
= *Myopopone* Roger, 1861:49. Type: *Myopopone castanea* var. *maculata* = *Myopopone maculata* Roger = *Amblyopone castaneus* Fr. Smith, 1860, by designation of Bingham, 1903.

In general habitus, to the naked eye, *Myopopone* workers look very much like those of *Amblyopone australis*, and they show variation of similar scope. In fact, *Myopopone* is probably monotypic [20], and may be regarded as a more than usually

aberrant species of *Amblyopone*. The characters are, however, sufficiently marked and numerous in the worker-female castes to justify the retention of *Myopopone* as a genus apart from *Amblyopone*. The head shape (Fig. 10) is like that of *Amblyopone*, without the "amblyoponine teeth" at the corners anteriorly, but the lobes of the frontal carinae are large and placed well forward, so as to overreach slightly the concave median lobe or apron of the clypeus (in *Amblyopone* the lobes never reach the anterior border of the median clypeal lobe). The antennal funiculi are strikingly broadened and flattened, differing in this from *Amblyopone*. The legs are short and with spiniform processes or spine-like setae developed at several points; in particular, the extensor surface of the middle tibia is provided with a number of sharp peg-like spines, also the metatarsus of the posterior leg. The mandibles, as can be seen from Figure 10, are different from those of any given species of *Amblyopone*, but are not strikingly outside the range of variation seen among *Amblyopone* species.

The female is winged and is markedly larger and darker than the worker; there are also differences in sculptural detail. The differences between these two castes have been responsible for much of the synonymy at species level. The male is decidedly smaller and more slender than the female, and is typically amblyoponine in its habitus and general characters, with rugulose head and alitrunk and piceous to blackish in color. Notauli present.

Pygidium and subgenital plate both subtriangular, with broadly rounded apices. Parameres rather long, tapered and incurved so that their apices meet or even slightly overlap at the half-retracted position. Volsellae (Fig. 12) much like those of *Amblyopone australis* (Fig. 9); digitus with a flat, plate-like apical portion, which is convex and tuberculate over its lateral surface; cusp reduced to a vestigial swelling at the base of the digitus, but the heel well developed and bearing a sharp erect tooth. Aedeagus of a peculiar shape, as shown in Figure 11. In all castes, the middle and posterior tibiae have two pairs of spurs, one of the posterior pair being larger than its mate, slender, curved, narrowly barbulate and with a peculiar obliquely truncate tip. Antennae stout, but not flattened as in the worker.



Myopopone castanea. Figure 10. Head of worker, full-face view (from type series of synonymous *M. rossi* Donisthorpe, Finschafen, New Guinea). Figure 11, aedeagal valve of male from Pematang Siantar, Sumatra. Figure 12. Volsella of same specimen, ventral view. Figure 13. Volsella in place in left paramere, viewed from midline, aedeagal valve omitted; same specimen. Figure 14, sub-genital plate of same specimen.

Workers and females with 4 maxillary and 3 labial palpal segments. Wings in both sexes similar to those of "complete-veined" *Amblyopone* species, narrow, glassy, with dark veins; Mf2 usually completely or nearly completely contracted in forewing.

I consider that the present evidence **[20]** indicates the probability that all of the *Myopopone* specimens so far collected belong to one species, *M. castanea* (Fr. Smith), which ranges from Sikkim, Ceylon, and the Nicobars in the west to the Philippines, New Guinea through the Solomons, and central Cape York Peninsula of northern Australia in the east. In Melanesia, *M. castanea* is predominantly a lowland species, occurring mostly at or below 500 m.; apparently it replaces *Amblyopone australis* in this zone. *A. australis* in Melanesia is predominantly a mid-mountain rain forest species, living chiefly at altitudes of 1000 m. or more. In southeastern Asia and the Philippines, where no similar *Amblyopone* species is known to exist, *M. castanea* exists at altitudes up to more than 2000 m.

M. castanea, like rain forest populations of *A. australis* found in the tropics, inhabit rotting logs, where they feed on large beetle larvae and probably on other comparatively helpless arthropods. Wilson's observations indicate that, as in the case of at least some *Amblyopone*, the colonies are very loosely organized, and that the workers may bring their brood to the site where the prey has been found, stung and killed, rather than attempt removal of the largest kinds of prey to a central nest or brood area. As has been suggested, such behavior may grade into primitive nomadism (Wilson, 1958 a, b).

Prionopelta Mayr

= *Prionopelta* Mayr, 1866:503. Type: *Prionopelta punctulata* Mayr, 1866, monobasic (+9 spp.).

> *Renea* Donisthorpe **[23]**, see under *P. majuscula*.

> *Examblyopone* Donisthorpe **[23]**, see under *P. majuscula*.

When Mayr originally described *Prionopelta*, he demonstrated clearly the amblyoponine affinities of the sole species then included (*P. punctulata*), rendering inexplicable Emery's later placement of the genus in tribe Ectatommini. Wheeler (1922) followed Emery in this placement, making it "generally accepted." But when the relationships of the known *Prionopelta*

species are seriously studied now, there is simply no question about Mayr's opinion that *Prionopelta* is close to *Amblyopone*. In fact, the characteristic narrow, short, 3-toothed mandible is the only thing really consistently marking *Prionopelta* (Fig. 15)

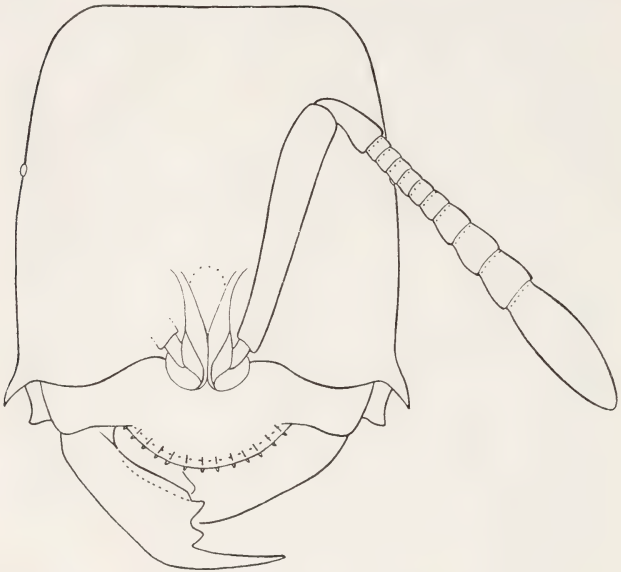
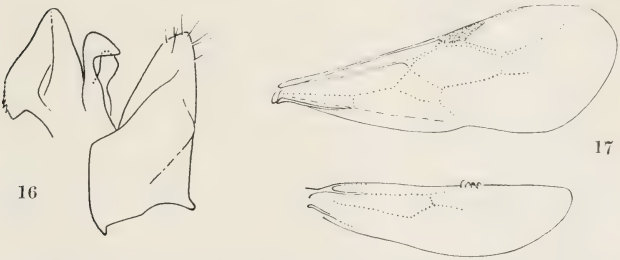


Figure 15. *Prionopelta brocha*, full-face view of holotype worker.

off from *Amblyopone* of the *Fulakora* group of species, as represented by *A. smithi* (Fig. 40). Except in *P. brocha*, which is very *Amblyopone*-like in everything but mandibular structure (Fig. 15), the *Prionopelta* species run to more nearly parallel-sided heads, usually broadest near the middle; that is, not broadest anteriorly near the anterior corners. The genal tooth at the corner on each side is, again with the exception of *P. brocha*, absent or present only as a minute vestige.

The anterior clypeal border is normally convex or moderately projecting and armed with a row of inconspicuous denticles corresponding to the clypeal armament of *Amblyopone*. The eyes are small to minute in the worker, moderate-sized in the female, and are normally placed behind the middle of the sides of the head in both worker and female. The antennae are 12-segmented in worker and female, or more rarely 11-segmented; apical 3-4 segments incrassate, forming a more or less distinct club. Male antennae 13-segmented, filiform, with feebly thickened apex; scape very short. Maxillary and labial palpi both 2-segmented in



16 17

Prionopelta punctulata male from Tucumán, Argentina. Figure 16. Left aedeagal valve, volsella and paramere, partly detached as flattened on slide. Figure 17. Wings.

all castes. Male mandibles like those of *Amblyopone*, 2-toothed. Notauli present in male. Genitalia of male not unusual in shape (Fig. 16); volsella without second cusp. Wings as shown in Figure 17, though the veins are more distinct in some species. The female usually has slightly heavier and more complete venation than in the male of a given species. Variation extends to Mf4, which may be completely lacking (e.g., *P. kraepelini* female), and to CuA in the hindwing, present in the females of some species as a distinct spur (e.g. *P. majuscula* female).

The *Prionopelta* species are all small to minute in size, and mostly have depigmented (testaceous to reddish-brown) workers, though in some species (e.g., *P. majuscula*), the female is piceous. Males are black or piceous; the three castes are usually

similar in size (length), but in *majuscula,* the female is distinctly larger. The sculpture consists of close punctulation, varying in coarseness with the species, but most distinct on the dorsum of the head, and weakening posteriorly toward the gaster, the last usually being wholly or in part smooth and shining. Pilosity simple, short, reclinate to erect, usually rather abundant.

The characteristics of the worker *Prionopelta* are mostly adaptations indicating a cryptobiotic mode of life, and the direct information available on the ecology of several species all goes to show that these are inhabitants of the soil and soil cover. Most of the species are at home in moist tropical forest, but some of them can survive in semiarid areas such as northwestern Argentina (Kusnezov, 1955: 276) by keeping to a strictly hypogaeic mode of existence in the moister microhabitats. Kusnezov (*loc. cit.*) has questioned the inclusion of the Old World *Prionopelta* species in one genus with those from the New World, but I see no reason to question the judgment of older authorities in this matter. Leaving the somewhat primitive *P. brocha* to one side, the present species of *Prionopelta* form an exceptionally homogeneous group so far as we can tell from the known examples of all castes and from the known biology. *P. brocha,* while sharing a number of characters with *Amblyopone,* is nevertheless clearly a *Prionopelta* in the form of the mandibles. Since the mandibular differences are complex ones that have probably accompanied an adaptive shift (in feeding habits?) of some significance, I see no need to exclude *P. brocha* from *Prionopelta.*

The characters of *Prionopelta* include many that are reductions from average or primitive characters of *Amblyopone,* so that it seems likely that the latter is the parent genus. In the tropics of both hemispheres, *Prionopelta* appears to be distributed geographically and ecologically roughly so as to replace the smaller *Amblyopone* of the "*Fulakora*" group. As examples of this may be cited New Guinea (with two widespread *Prionopelta* species) and the Solomons (with *Amblyopone celata*) plus southeastern Australia (with several of the small "*Fulakora*" species). A somewhat similar situation apparently holds in the American tropics, where in some areas *Prionopelta* is very common **[21],** but the smaller, depigmented *Amblyopone* species are either unknown or tend to be restricted to geographically or ecologically peripheral ranges.

Prionopelta, on the other hand, does not extend significantly into the temperate or cool montane regions (except perhaps in Australia), and is represented on the Asian-African mainlands only by a single collection from Zululand. So far as is known, of course, amblyoponines are in general very poorly represented in Africa below the Sahara, and no species have yet been found in the Congo rain forests. *Prionopelta* ranges in the New World from southern Mexico south into northwestern Argentina, in the West Indies extending only into the Lesser Antilles, where *P. antillana* may be introduced. In Cuba, a small species of *Amblyopone* that has been collected only once may take the place of the absent *Prionopelta* **[7]**. Two species of *Prionopelta* are widespread and fairly abundant in New Guinea, but these tend to have different ranges within the area, or at least different modes of abundance. One of the species, *P. opaca,* has a close counterpart in the East Indies (Java) and the Philippines (*P. kraepelini*), and these two species may intergrade in the Micronesian islands, where they have probably been introduced by man **[23]**. The curious species *P. brocha* is known only from the type collection on New Caledonia. Since New Caledonia appears to have received by far the greatest bulk of its ant fauna by way of eastern Australia, the recent discovery of a species in Queensland **[23]** is not surprising. In this connection, the little-known *Dorylozelus* must be re-examined (see below).

Prionopelta Species

aethiopica Arnold, 1949, Occ. Pap. Nat. Mus. S. Rhodesia, 2(15):263, fig. 4, 4a, worker. N. status. Zululand. **[23]**

(T) *amabilis* Borgmeier, 1949, Rev. Brasil. Biol., 9:203, figs. 3-5, worker. Costa Rica. **[21]**

(T) *antillana* Forel, 1909:239. N. status. Lesser Antilles, n. S. America, etc. **[21]**

(T) *brocha* Wilson, 1958a:147. New Caledonia. **[23,** Fig. 15]

descarpentriesi Santschi, 1924, Rev. Zool. Afr., 12:195, worker. Madagascar. **[23]**

(P) *kraepelini* Forel, 1905, Mitt. Naturh. Mus., Hamburg, 22:3, female, worker. E. Indies, Philippines, Micronesia. **[23]**

(P) *majuscula* Emery, 1897:595. N. Guinea & nearby islands. (= *Ponera simillima* Fr. Smith, *Prionopelta poultoni* Donisthorpe, *Renea testacea* Donisthorpe, *Examblyopone churchilli* Donisthorpe, synonymized by Brown, 1953b:12; see also Wilson, 1958a:148.) **[23]**

(P) *modesta* Forel, 1909:241. C. America, s. Mexico. [21, 22]
(T) *opaca* Emery, 1897:596. N. Guinea, Micronesia, Australia. [21, 23]
(T) = *mocsaryi* Forel, 1907, Ann. Mus. Nat. Hungar., 5:1, worker. Synonymized by Brown in Wilson, 1958a:149.
(P) *punctulata* Mayr, 1866:505. s. Brasil, n. Argentina. [21]
(P) = *mayri* Forel, 1909:239. N. syn.
(P) = *bruchi* Santschi, 1923, Rev. Suisse Zool., 30:245, "female" (*recte* worker?). N. syn.

Onychomyrmex Emery

Onychomyrmex Emery, 1895:349. Type: *Onychomyrmex hedleyi* Emery, 1895, monobasic.
Onychomyrmex, Forel, 1915:2, characters.
Onychomyrmex, Wheeler, 1916; revision of genus, ecology, ethology, larva.

This genus evidently represents a development of the army-ant or legionary life-form that has arisen independently from an Australian *Amblyopone* stock. The worker of *Onychomyrmex* (Figs. 46, 48) is accordingly more slender and has longer appendages than is usual for *Amblyopone*, and the integument is smooth and shining, the mandibles more down-curved and hook-like, and the tarsal claws much enlarged, particularly those of the last two pairs of legs. The spurs of the posterior pair of tibiae are reduced to minute, straight, almost setiform vestiges, or else are lacking altogether. In *O. hedleyi*, the spur vestiges may be present or absent in different workers from the same nest. To complete the resemblance to certain true army ant genera (subfamily Dorylinae) the *Onychomyrmex* female (known for two of the three species) is dichthadiiform, that is, it has the head peculiarly broadened, very small eyes, workerlike alitrunk without wings or corresponding sclerites, and elongate, bulky gaster.

Despite these characters, which misled Emery and most other authors to consider the genus as an aberrant and independent tribal group within subfamily Ponerinae, the amblyoponine affinities are so clear that one wonders why it was so long before they were properly interpreted. The mandibles, clypeus, position of the eyes on the posterior half of the sides of the head, the long sting, and the basic form and structural relationships of alitrunk, petiole, postpetiole and remainder of gaster in the worker are all unmistakably amblyoponine. The larva also shows

no features that seem to contradict an amblyoponine affinity (Wheeler, 1916; G. C. and J. Wheeler, 1952: 637), although the Wheelers consider it to show specialization in the direction of the Cerapachyinae larva.

Males from southeastern Queensland are believed to belong to *O. mjoebergi;* these are similar in size to the worker, and have the general characters of some of the slender small *Amblyopone* species. The wing venation is shown in Figure 47; the genitalia are peculiar in having short, broad parameres, which are bent sharply inward, then caudad, the apical portion forming a curved vertical plate on each side with a cultrate transparent margin. The subgenital plate is narrowly tongue-shaped and projecting at its apex. The sculpture is predominantly smooth and shining. Mandibles with 2 apical teeth; palpi segmented 2,2.

John Clark (1928) was the first to relate *Onychomyrmex* to *Amblyopone* unequivocally when his relict *Lithomyrmex* (now *Amblyopone*) *glauerti,* from Western Australia, turned up and was recognized as intermediate between *Amblyopone* and *Onychomyrmex* in many worker characters. *A. glauerti,* however, has a normal winged female, and in other ways follows *Amblyopone* so closely that I was unable to separate it from that genus. On the other hand, the intermediacy of *A. glauerti* confirms beyond reasonable doubt the amblyoponine affinities of *Onychomyrmex.* Emery's position in isolating *Onychomyrmex* can be explained, I think, by his belief in the taxonomic significance of the tibial spurs. At present, we know that these spurs are not always reliable classificatory guides, particularly among the Ponerinae. Clark's paper appears to have been seen by few myrmecologists, and *A. glauerti* by still fewer, so Emery's and Wheeler's classifications have in the main been followed until very recent years.

As now known, *Onychomyrmex* has three species, all occurring in eastern Queensland in rain forest, chiefly in rotten logs. Probably the genus extends into northeastern New South Wales. It is much rarer in the southern than in the northern part of its range.

Wheeler (1916) relates his finding workers of *O. mjoebergi* "biting and stinging to death a huge lamellicorn beetle larva more than two inches in length, which they had just found in a

cavity'' in a rotten log. It is not clear from Wheeler's account whether the beetle larva was attacked after he broke the log open, or before. Furthermore, it would seem that a two-inch lamellicorn (probably of family Passalidae, common in rotten logs in North Queensland rain forests) would be an impossible burden for even several hundred of the very small *Onychomyrmex* to move through the narrow passages of the usual rotten log. Until the habits of *Onychomyrmex* can be checked in detail, it is interesting to speculate that the colonies of this genus may migrate from one large victim to the next, after subduing the prey by mass stinging attacks.

Wheeler found small companies of workers moving through logs in the manner of army ants mass-foraging, and I myself have found aggregations answering this description well in the species *O. hedleyi* and *O. doddi*. One party of *O. hedleyi* found in a log at Malanda on the Atherton Tableland numbered several hundred workers, without queen or brood.

The behavior of these workers reminded me very much of the actions of foraging groups of *Leptogenys* and *Aenictus* that I have seen in Australia, Western China and Assam. A colony of *O. mjoebergi* found by Wheeler at Kuranda ''comprised at least 400 workers, a single queen, with the abdomen greatly distended with eggs, and a large number of nearly mature larvae but no pupae.'' These circumstances suggest that *Onychomyrmex* may resemble the New World army ants studied by Schneirla in having brood-rearing and nomadism synchronized.

Key to the Species of Onychomyrmex — workers

1. Mandibles predominantly smooth and shining, with a few coarse punctures; robust species, with broad head (CI usually > 78); color yellowish-red to reddish-brown ..... *mjoebergi*
   Mandibles densely striate above; more slender species, with narrower head (CI usually < 78) ..... 2.

2. Larger species; length of alitrunk (WL) > 1.2 mm.; full adult color black or dark piceous ..... *hedleyi*
   Smaller species; length of alitrunk (WL) < 1.2 mm.; full adult color deep reddish-brown ..... *doddi*

Onychomyrmex Species

(T) *doddi* Wheeler, 1916:53. n. Queensland [**24**]
(T) *hedleyi* Emery, 1895:350. e. Queensland [**24**, Figs. 46, 48]
(T) *mjoebergi* Forel, 1915:2. e. Queensland [**24**, Fig. 47]

INCERTAE SEDIS

Paraprionopelta Kusnezov

= *Paraprionopelta* Kusnezov, 1955:270. Type: *Paraprionopelta minima* Kusnezov, 1955:271, figs. 1, 2, 5a, male; monobasic.

This monotypic genus was based on males taken separately, presumably at light, at Tucumán, Argentina. These males are minute (under 2 mm. TL), dark in color, and have a somewhat *Amblyopone*-like petiole. They differ from the known males of Amblyoponini in the oblong shape of the head, in the shape of the mandibles, and especially in having 10-segmented antennae. There are no distinct teeth on the anterior clypeal margin, but the hind tibiae do bear broadly pectinate spurs. Possibly this genus really is an amblyoponine, but since a similar type of petiole occasionally appears convergently in other groups of ants, I do not consider this a certainty. If it is in the Amblyoponini, then one is tempted to match it with the worker of *Amblyopone degenerata* from southern Brazil; the two are similar in size, and both have reduced antennal segmentation.

Dorylozelus Forel

= *Dorylozelus* Forel, 1915:24. Type: *Dorylozelus mjoebergi* Forel, 1915:25, fig. 4, worker; monobasic.

This genus is known only from the type (or types?) of *D. mjoebergi*, taken by Mjöberg in the Blackall Range in southern Queensland. Despite all efforts to locate the type material in the Forel Collection at Geneva, in the Naturhistoriska Riksmuseet in Stockholm, and in various Australian collections, it could not be found.

Failing in the effort to find the type, I spent a week searching the rain forests in and around the Blackall Range for more specimens, but found none. T. Greaves and the Darlingtons have also looked for *Dorylozelus* in the Blackalls without success. It is important that this ant be rediscovered, and the sexes and larvae examined, because its systematic position at the moment

is anything but clear. Wheeler placed it in a separate tribe Dorylozelini, but probably he never saw a specimen of *D. mjoebergi*.

As characterized by Forel, this species is a mixture of characters like those of *Dorylus* and *Ponera*. The petiole and gaster are supposed to be like those of tribe Ponerini. The frontal lobes are contiguous, as in Ponerini, but also as in some amblyoponines. The mandibles, as drawn by Inez Forel, are like those of *Prionopelta* in general pattern, narrow and straplike, with three apical teeth, of which the middle tooth is smallest. The antennal funiculi are incrassate, with only 10 segments. Inez Forel's drawing is highly diagrammatic and difficult to interpret. One even wonders whether there is any possibility that the specimen is a compound one, so disharmonious is the image created by the original characterization. *Dorylozelus* remains one of the most puzzling anomalies among the ants. Only with more material will we be able to place it more satisfactorily.

APPENDIX

The pages of this appendix are reserved for notes and descriptions dealing chiefly with species-level taxonomy and biology. In the descriptions, the abbreviations for measurements and indices are as follows: TL, total outstretched length of body, including mandibles (sum of all tagmata); HL, maximum measurable length of head, including clypeus, but not mandibles; HW, maximum measurable width of head, ignoring eyes if present (head measurements are made from dorsal full-face view); CI, or cephalic index, is HW/HL $\times$ 100. WL, or Weber's length, is the diagonal length of the alitrunk as measured from side view. L, of course, generally stands for length, and W for width (in mm.).

Places where types or other specimens are deposited are indicated within brackets where convenient, especially the abbreviation MCZ, which stands for the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts.

[1] Borgmeier (1957: 108-112) has discussed *A. armigera* and *A. elongata* and brought their descriptions up to date. His synonymy for *elongata* is followed here. He found the worker of *elongata* to have the palpi segmented 3, 2.

Kusnezov's *Ericapelta egregia*, described from isolated males, is about the right size to be the male of *A. armigera*, and I expect that association of the sexes will eventually prove this synonymy.

A. chilensis has been collected by Ross and Michelbacher in southern Chile on the northern shore of Lake Llanquihue and in valley forest 18 km. west of Purranque, both localities to the south of the type locality, Valdivia.

[2] *Amblyopone pallipes* is a rather common ant in forested areas of the eastern United States and in the St. Lawrence Valley near Montreal. Brown (1949:84) has shown that the subspecies *montigena* Creighton is based on individual nest variants occurring sporadically in the eastern United States. In the 1949 paper, *subterranea* Creighton, based on samples from deep subterranean collections made in the plains states, was raised to species rank on the basis of what were thought to be diagnostic sculptural characters. Now, however, after the examination of many more collections from all over the eastern United States and the Mississippi Valley, and considering samples from Arizona (near base of Huachuca Mts., R. G. Wesson leg.) and Iowa (W. F. Buren leg.), it appears that the characters thought in 1949 to be diagnostic of a distinct species are in fact only average differences, connected by clinal variation to the eastern characters. Actually, the differences are slight; the underlying pigmentation affects the appearance of the fine sculpture. Samples from the Plains are frequently lighter in color than those from the eastern forests, but even some samples from the eastern coastal areas are medium brownish-ferruginous in color.

Although it may be that the distribution of *Amblyopone* is continuous between Arizona and the Plains and the Pacific Coast, we have no records between Arizona and northern California, where the population of *oregonensis* commences and runs northward through the moist coniferous forest belt. Although *oregonensis* has been considered to be a subspecies of *pallipes*, the differences between the two remain constant so far as known, and I shall call *oregonensis* a species until we have more information on possible range contacts between it and *pallipes*.

On several occasions in eastern Massachusetts, *A. pallipes* has been observed under stones in hardwood forest together with

dead centipedes, usually lithobiids or geophilomorphs. The association in each case left no doubt that the ants were using chilopods for food; usually larvae were attached to the centipedes and appeared to be feeding actively. In another case, W. L. Nutting found *A. pallipes* workers attacking an asilid larva in leaf litter. Most observers agree, however, that chilopods are the main source of food for this species. In my experience, the centipedes used for food showed considerable variability in size and form, and lithobiids many times the size of the ant are found with the ants as often as smaller prey. It is assumed that

Figure 18. *Amblyopone trigonignatha*, holotype worker, dorsal view of left mandible and anterior clypeal apron.

the long, sharp sting of *A. pallipes*, which can penetrate even the human skin in some places, is used to subdue living prey, but we do not know all of the details of hunting behavior. *A. pallipes* workers in the artificial nest are very timid, and can scarcely be stimulated to attack centipedes of any kind enclosed with them.

When the ants are found with dead centipedes in the field, it usually is in a situation under a stone such that transport of the prey by the ants seems unlikely. I believe that the larvae are often brought to the spot where the larger sort of prey dies,

and that they feed there for considerable lengths of time, rather than the reverse situation usual for ants, where the food is brought by the ants into more or less central brood chambers.

[3] *A. trigonignatha* was described in 1949 from a single worker taken in a leaf mold berlesate from Concord, North Carolina. It is very distinctive in the form of the clypeus and mandibles (Fig. 18). More than 200 separate collections of *Amblyopone* from all over the eastern half of the United States have been examined since 1949, but all these proved to be the common *A. pallipes*. *A. trigonignatha* still remains known only from the holotype [MCZ].

[4] AMBLYOPONE MYSTRIOPS sp. nov.
(Fig. 19)

Holotype female (alate): TL 7.2 (gaster expanded), HL 1.47, HW 1.38 (CI 94), WL 2.21, petiole L 0.66, petiole W 0.76, scape L (without basal neck) 0.91, straightline outside L left mandible 1.50, forewing L 4.3 mm.

Habitus and details of head, mandibles and scape as in Figure 19. Frontal lobes distinctly separated by an extension of the clypeus and the pit-like "frontal area." Genal teeth reduced to low rounded eminences. Clypeal apron short, convex, with 8 slender oblique teeth. Mandibles as shown in the figure; broken line on each shaft represents a rather indefinite dorsal carina or costa; between this and the tooth rows, the surface is concave. Viewed from the side edge-on, the mandibles are seen to be markedly flattened in an oblique ventrolateral direction, and the apical quarter is incrassate. Note the low, inconspicuous basal lamella, the small size of the apical tooth, and the convex ridge or swelling formed ventral to the subapical teeth, near the apex: the principal (median) teeth on the blade are in two separate ranks.

Antennal scapes curved and arched, slightly narrowed toward their midlength. Funiculus slightly but gradually thickened toward apex; segments I through VI longer than broad, I (pedicel) about 1½ times as long as II through X, which are approximately equal among themselves in length; VII and VIII about as long as broad; IX and X slightly broader than long;

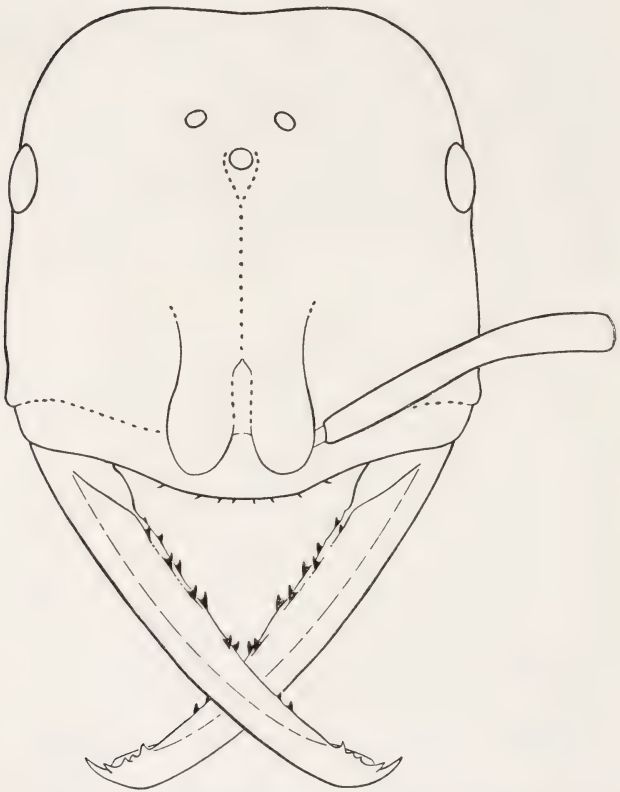


Figure 19. *Amblyopone mystriops*, holotype female, full-face view of head, including mandibles and left antennal scape.

XI (apical) twice as long as X. Under-mouthparts retracted, but 3 segments of the maxillary palpi and a single segment of each labial palpus are exposed; probably there are more basal segments hidden beneath the folded labrum.

Alitrunk very similar to that of large females of *A. pallipes*. Petiole also similar, but a little broader, with a nearly vertical anterior face, slightly concave in profile, rounding sharply into the gently convex dorsal face. Seen from above, the front and side outlines of the node are convex, although the front is slightly indented in the middle. Ventral process as in *A. pallipes*. The (normally exposed portion of the) postpetiole is a little longer than the petiolar node, and distinctly wider; abdominal segment IV is slightly longer and wider than III (postpetiole). Apex of gaster slightly laterally compressed; sting slender, curved.

Sculpture of head much like that of *A. pallipes*, reticulate-punctate and predominantly opaque; on anterior half of head, some of the interpunctural ridges form fine, parallel costulae on the lower, inner genae and on the frontal carinae, but these less distinct and extensive than those of *pallipes*. Cervical face of occiput shining, punctate. Clypeus longitudinally striate; "frontal area" a round-bottomed pit, smooth and shining, as is also a small impression in front of the anterior ocellus. Mandibles coarsely oblique-longitudinally striate, moderately shining. Antennae, tibiae and tarsi densely punctulate, subopaque. Alitrunk densely punctulate, shining (punctures not contiguous), the punctures rare on the pleura; lower half of lateral propodeal surfaces coarsely longitudinally striate; declivity smooth. Petiole, gaster and femora smooth, shining, with spaced punctures, those on the postpetiolar disc trailing shallow sulci.

Pilosity consisting mainly of soft, reclinate to oblique, pubescence-like hairs, densest on head, legs and gaster, but not hiding sculpture. Longer fine hairs on mandibles (especially inner surfaces), front of head, antennae (including scapes), legs and apex of gaster. Head and body dark reddish brown to piceous; mandibles, antennae and legs sordid yellow.

Wings hyaline, with yellowish veins and dark brown pterostigma in forewing. Venation of forewing of the "complete" type, without first radial crossvein. Rs joining wing margin ("radial cell closed"), Mf4 short, Mf2 present but short.

Holotype [MCZ] a unique female found among unidentified miscellany; labelled: "Guatemala:/Los Amates/Kellerman." Presumably this refers to Los Amates in the valley of the Rio Motagua, near the Honduras border.

In the form of its mandibles and their dentition, this species differs widely from all other *Amblyopone* species, and makes an approach to the condition in *Mystrium* (compare Figs. 4 and 19). The pilosity and other characters are, however, typical for *Amblyopone* rather than *Mystrium*. Whether this aberrant species represents a phyletically transitional form, or merely a New World convergence toward the *Mystrium* type, I cannot say. It would be interesting to know more about the habits and ecology of this odd species.

[5] AMBLYOPONE MONROSI sp. nov.
(Fig. 20)

Holotype worker: TL 4.3, HL 0.92, HW 0.77 (CI 84), WL 1.19, petiolar node L as seen from above 0.47, petiole W 0.43, scape L without basal neck 0.51, exposed straight-line outside L of left mandible 0.54 mm.

Amblyopone species, dorsal views of anterior border of clypeal apron. Figure 20. *A. monrosi*, paratype worker. Figure 21. *A. bruni*, holotype of synonymous *A. bruni juergi*.

A rather typical-appearing smallish *Amblyopone* of the "*Fulakora* group," with sides of head gently convex, posterior border weakly concave, greatest width of head at about the anterior third. Genal teeth acute, but small and almost hidden in pilosity. Compound eyes represented by a small patch of unpigmented, indistinct facets in the usual position. Frontal lobes small, contiguous, the line of separation deeply impressed. Clypeal apron with corner teeth unusually large and broad, blunt at apices and projecting over the masticatory borders of the closed mandibles (Fig. 20). Between the corner teeth are 6 smaller, obliquely truncate teeth socketed on low tubercles, the two median teeth about even with the apices of the corner teeth. (One or both of the outer small teeth may be fused to the corner tooth adjacent in different specimens.)

Mandibles basically of the typical *Amblyopone* pattern, but shorter and broader than usual, especially the thick, blunt-tipped apical tooth. Inner margin convex. Basal quarter or so of masticatory border occupied by a round-edged translucent lamella, about as high as the acute double teeth. The right mandible (crossed above the left in both holotype and paratype) has a small single tooth following the lamella, and after this, at the midlength of the mandible, a large, slightly retrorse double tooth; after this three large, apparently single teeth before the apical tooth. The left mandible, after the basal lamella, has three moderate-sized double teeth, followed by two subapical single teeth. (The paratype has similar dentition.)

Antennal scapes short, thick, only very slightly curved and feebly incrassate toward apex. Funiculus 11-segmented, strongly incrassate toward apex, but thickened gradually from segment II on to apex. All segments except the pedicel (I) and the apical (XI) appear to be broader than long, though VI, VII, VIII and IX are only slightly so. Apical segment almost as long as the preceding 3 segments taken together.

Alitrunk slender, straight in dorsal profile, rounded downward gently at the front of the pronotum and, posteriorly, into the plane, sloping declivity. Mesonotum almost twice as broad as long; promesonotal suture impressed; metanotal groove present but not conspicuous. Seen from above, the mesonotal area is gently constricted. Petiole seen from above subcircular, truncate behind. Seen from side, anterior face steep, curving broadly into gently convex dorsum. Ventral lobe rounded, with a long posterior slope. Postpetiole only a little longer than petiole, and only a little wider in its posterior part. Next segment (abdominal IV) slightly longer than postpetiole, and slightly wider, making the widest part of the gaster. Remainder of segments tapering caudad, subconical; sting stout, curved.

Body with head predominantly smooth and shining; head with abundant, small, close but not contiguous punctures, becoming much feebler and fewer on alitrunk and especially on gaster. Lower 2/3 of sides of propodeum and most of upper mandibular surfaces longitudinally striolate. Antennae very finely and densely punctulate, opaque.

Erect pilosity generally distributed, rather sparse and short, becoming a little longer and more abundant near gastric apex. Accompanying the longer pilosity, and replacing it on the legs, is a short fine reclinate pubescence. Color yellowish ferruginous.

The holotype [California Academy of Sciences] and the very similar paratype worker [MCZ] were taken together about 10 miles northeast of Pucon, Chile, by E. S. Ross and A. E. Michelbacher. This species is readily separated from *A. chilensis* by the shining sculpture of the head and the different clypeal and mandibular armament. Differences from other New World species are given in the key. This is the second species to be found in Chile.

The name is given in memory of my late good friend, Dr. Francisco de Asis Monrós, of Tucumán, Argentina, whose tragic death has deprived the world of a gifted and devoted scientist.

[6] AMBLYOPONE ORIZABANA sp. nov.

Holotype worker: TL 2.7, HL 0.58, HW 0.48 (CI 83), WL 0.74, petiole L 0.26, petiole W 0.29, scape L (without basal neck) 0.31, straightline outside L of left mandible 0.34 mm. A very small, yellow member of the "*Fulakora* group" with dorsum of head densely and evenly reticulate-punctate and opaque or nearly so. The habitus and shape of head, body and appendages are all substantially as in *A. smithi* [**17**, Fig. 40], although the posterior occipital border is more strongly concave in the middle in *orizabana*. Also, the mandibles are more slender in *orizabana*, and can close tightly against the clypeal apron (as in the holotype). Clypeal apron convex, with 4 truncate teeth socketed on low tubercles in the middle (median pair smaller, bases fused), flanked by broader corner teeth on each side; the latter cannot be seen clearly, and may possibly be subdivided. The mandibular dentition is difficult to see, but it appears to consist of a triangular basal tooth or lamella, 4 sharp double teeth, and a reclinate, acute subapical tooth in addition to the slender apical tooth. The inner borders are convex. Antennae much as in *A. smithi*.

Alitrunk constricted at the narrow, transverse mesonotum, which is continuous with the propodeal dorsum; metanotal groove almost obsolete, visible only in certain lights. Petiolar node with a vertical anterior face, convex in both directions;

dorsum only weakly convex. Petiole and postpetiole about equal in length; abdominal IV slightly longer. Ventral process of petiole with a small angular anterior lobe and a larger, bluntly subtriangular posterior lobe that slopes upward gradually posteriad. Gastric apex not compressed; sting stout.

Mandibles and lower sides of posterior half of alitrunk longitudinally striolate. Underside of head densely reticulate-punctate, but weakly shining. Rest of body, including legs, scapes and frontal groove, smooth and shining, with numerous, spaced small piligerous punctures, best seen on pronotum and petiole. Pilosity fairly abundant, but very short and mostly oblique; longer hairs on mandibles and gastric apex. Color light ferruginous yellow.

The holotype, a unique [MCZ], was taken by E. O. Wilson on Pico Orizaba, Veracruz, Mexico, on August 24, 1953. The worker was found under a large mossy rock in an open grassy strip along the trail between La Perla and Rancho Somecla, on the southern slope of the mountain, at about 2700 to 2800 m. altitude. At this altitude, the original forest cover is mainly broadleaf temperate trees, with *Carpinus* abundant and some pines. This rather ordinary small *Amblyopone* is easily distinguished from all the American species by its small size and yellow color; only *A. degenerata* is smaller, and this is very different in antennae and sculpture.

[7] *Key to the New World Species of Amblyopone — Workers and Females*

1. Antennae 7-segmented; worker eyeless, minute, yellow in color (holotype only 1.7 mm. total outstretched length) (se. Brazil) *degenerata* Borgmeier

   Antennae 12-segmented; worker larger, usually over 2 mm. in outstretched length ..... 2.

2. Lobes of frontal carinae separated by a distinct gap (Fig. 19) ..... 3.

   Lobes of frontal carinae contiguous or fused, as in Figure 40 ..... 6.

3. Mandibles on inner surfaces each with two sparse separate rows of small, sharp teeth (Fig. 19, Guatemala) ..... *mystriops* Brown

   Mandibles on inner surfaces with much larger teeth, those near the midlength fused at their bases so as to form heavy double teeth (Figs. 18, 40) ..... 4.

4. Inner borders of mandibles angulately produced, so that the blades are triangular in shape without the apices; large double teeth with rounded apices; genal teeth reduced to inconspicuous obtuse angles (Fig. 18; Piedmont of North Carolina) ..... *trigonignatha* Brown
Inner borders of mandibles straight to convex, not angulately produced, the blades linear; large double teeth predominantly acute; genal teeth acute and projecting ..... 5.

5. Inner borders of mandibles and anterior clypeal apron straight, or at most only feebly convex (n. California to Brit. Columbia) *oregonensis* (Wheeler)
Inner borders of mandibles, and usually also the anterior clypeal apron, decidedly convex in outline (temperate N. America w. at least to Iowa and Arizona) ..... *pallipes* (Haldeman)

6. At least the anterior 3/5 of the head (as seen in full-face view) predominantly densely sculptured and opaque ..... 7.
Entire or nearly entire dorsal surface of head smooth and shining, with spaced punctures ..... 10.

7. Anterior 3/5 to 3/4 of dorsum of head coarsely longitudinally striate with intermixed punctures, occiput smooth and shining, with spaced punctures; full adult color piceous or black (se. Brazil to n. Argentina) *armigera* Mayr
Dorsum of head densely and uniformly punctate or striolate-punctate and opaque throughout, except that the cervical border or median frontal groove may be shining in some cases; full color of worker yellow to ferruginous ..... 8.

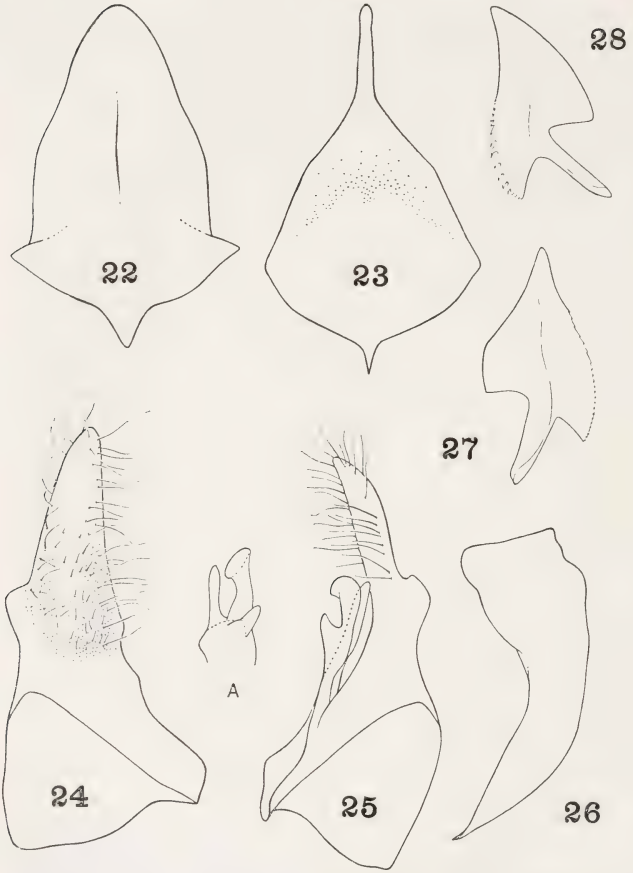
8. Size very small (TL of holotype worker 2.7 mm.); alitrunk very smooth, punctation sparse; propodeum with very few punctures on the dorsum, and its lateral striation restricted to the lower third of the sides; color of worker yellow (Mexico: Mt. Orizaba) ..... *orizabana* Brown
Size larger, TL of worker $>$ 3.0 mm.; punctures more abundant and distinct on alitrunk; sculpture of lateral faces of propodeum covering half or more of these surfaces ..... 9.

9. Size larger; unique holotype worker 4.5 mm. long (according to the original description) (Cuba) ..... *bierigi* (Santschi)
Size smaller; worker TL 3.0-4.1 mm., female TL 4.1-4.5 mm. (Chile) *chilensis* Mayr

10. Larger and more robust, worker head width $>$ 0.70 mm.; clypeal apron having the middle teeth small and not advanced beyond the much larger teeth that form the lateral corners (Fig. 20, Chile) .... *monrosi* Brown
Smaller and more slender, worker head width $<$ 0.60 mm.; clypeal apron convex in outline, the middle teeth distinctly advanced beyond the corner teeth (se. Brazil to n. Argentina) ..... *elongata* (Santschi)

[8] The large, relatively large-eyed, dark-colored workers with retrorse mandibular teeth in double rows (Fig. 3) form the group of *A. reclinata*. Belonging to this group are the nominal forms *reclinata, feai, rothneyi, bellii* and *quadrata*. I have been able to examine and compare directly the types of *rothneyi* and *bellii*, and I find them to differ scarcely at all. Forel's description of *bellii* is in error on several crucial points. First of all, the *bellii* types have denticulae on the anterior clypeal margin that are approximately as distinct as in the *rothneyi* type, and similar in form. The eyes of the *rothneyi* type are slightly larger (0.22 mm. greatest diam.) than in *bellii* (0.18 mm. greatest diam.), but not nearly so much so as Forel claims. I count about 70-90 facets in the *rothneyi* type before me (here designated and labeled as lectotype); though the count is very difficult, I find the two *bellii* syntypes to have almost as many facets (50-70) as *rothneyi*. In fact, under the best circumstances of counting, I seriously doubt whether the difference is significant.

The *bellii* types are slightly more coarsely and quite opaquely sculptured over head, alitrunk, petiole and postpetiole; in the *rothneyi* type, these areas are very densely punctate and nearly opaque, but many of the punctures do have narrow shining spaces between them, and the postpetiole is more definitely shining. Both of these species have the anterior genal angles bluntly subrectangular, and not projecting. The palpal count for both of the *bellii* syntypes is maxillary 4; labial 3 (not 2 and 3, as Forel states); the palpi cannot be seen in the *rothneyi* type. These two species may well be geographical variants; *bellii* is from Kanara, on the western side of the Peninsula south of Bombay, while *rothneyi* is from Barrackpore, near Calcutta. From Poona, central Madras Presidency, and Orissa, all on the Indian Peninsula, I have numbers of large males that probably belong to *bellii* and/or *rothneyi*. These males have distinctive genitalia and a long, narrow caudal process on the subgenital plate. The whole terminalia most resemble those of a series of large males of another species from Formosa (Figs. 23, 25), probably the same as the male doubtfully attributed to *bruni* by Forel (1913, Arch. Naturg., 79 (A6): 183), but which is more likely a member of the *reclinata* group.



Males of two indeterminate species of the *reclinata* group. Figure 22. Subgenital plate, specimen from Los Baños, Luzon (wings shown in Figure 5). Figure 23. Same, specimen from Chipon, Formosa (wings shown in Figure 6). Figure 24. Right paramere, mesial surface, and A, detached volsella in oblique view, Los Baños specimen. Figure 25. Left paramere with volsella attached, oblique dorsal view, Chipon specimen. Figure 26. Left mandible, Chipon specimen. Figure 27. Aedeagal valve, Los Baños specimen. Figure 28. Same, Chipon specimen.

There are several other series in the *reclinata* group in the MCZ. A series of workers from Mt. Makiling, Luzon (L. Uichanco leg.), and another accompanied by males from virtually the same locality (Los Banos, Luzon, F. X. Williams leg.) have small but protruding genal teeth, the apices of which are blunt or truncate. The sculpture of these two series is coarse and opaque, somewhat like that of the *bellii* types, and the eyes are about the size of *bellii*. However, the accompanying males have different terminalia; the subgenital plate (Fig. 22) has a broad, narrowly rounded lobe instead of the long, slender process of the males discussed above from India, which I take to be *A. bellii* on circumstantial evidence. A single male from San Carlos, Philippines, resembles the other Philippine males. The Philippine samples, and a series of workers of this same kind from Macao, were referred to *A. rothneyi* by Wheeler, but I think it is more likely that they are another species. Workers from both the Philippine and Macao series prove to have 5 segments in the maxillary palpi and 3 in the labial palpi, in comparison with the 4,3 count in the *bellii* types. A worker from the Cuernos Mts., near Dumaguete, Negros, Philippines, has small, protruding genal teeth, but the sculpture is somewhat lighter than in the Luzon and Macao series, more as in the *rothneyi* type. This specimen is smaller and has smaller eyes (greatest diameter about 0.14 mm.) with perhaps 35-40 facets, and agrees in this, in its smaller size, its sculpture, etc. with the description of *feai* by Emery.

Another small worker with rather small eyes, but this time with blunt genal angles like those of *bellii,* comes from Mao Marroe, 450 m., Soemba Island. This specimen is weakly shining over the alitrunk and quite shining over the petiolar node and postpetiole, these parts being cribrately punctate.

It is obvious that differences in eye size, petiolar width and so on are allometrically variable, and hence untrustworthy as species characters in the absence of more detailed information based on large series. Judging from the material before me, and taking into account the male characters, I would guess that the *reclinata* group consists of not less than two, and probably not more than three or four species. How the names are applied will of course have to be left to future revisers.

[9] Of the two forms described as *bruni* and *bruni* subsp. *juergi,* I have seen only the latter (holotype worker). When he described *juergi* in his "Glanures" paper, Forel apparently did not have before him the *bruni* type, and he probably used only the *bruni* description for the comparison. At any rate, he was wrong in describing the anterior clypeal margin of *juergi* as without denticulation; actually, very fine denticles are present. Of the other differences cited, at least some are allometric characters. Thus, relatively greater width of head and petiole and larger eye size are only to be expected of a larger worker as compared to a smaller one, as in this case. Since both of the types came from Pilam, Formosa (H. Sauter leg.), I think it likely that they are conspecific. This species has blunt double teeth on the mandibles, and the clypeal apron is characteristic in shape (Fig. 21).

[10] Two syntypes of *A. minuta* (type locality: Soengei Bamban, Sumatra, in termite nest) were examined through the courtesy of Dr. Besuchet. This is a very small species (TL 2.7 mm.) with slender mandibles; inner border feebly convex, teeth short, 3 double teeth with sharp retrorse points; apex slender. Clypeal apron nearly straight, with 6 separated teeth, inner two largest, outer two smallest. Head finely and densely reticulate-punctulate, opaque; alitrunk, petiole and gaster densely punctulate (apex of gaster less so), only moderately shining; the alitrunk subopaque. Color brown; appendages etc. yellowish.

A very small, dark brown male [MCZ] from Sandakan, Borneo (Baker leg.) may belong to this or a related species.

[11] Although they differ in size, the types of *luzonica* and *williamsi* in the Museum of Comparative Zoology are otherwise much more similar than the original characterizations and faulty figures indicate. In addition to the types, we now have further series from the Cuernos Mts. and vicinity, near Dumaguete, Negros Island, collected by J. W. Chapman and D. Empeso. This additional material, while closest to the *luzonica* type in size, somewhat bridges the gap between the two species. Considering the similarities, I cannot see that *williamsi* is more than a large "nest variety" of *luzonica.* Size differences of greater

magnitude occur between series in other species of the genus (e.g., *australis, denticulata, pallipes*). *A. luzonica* is related to *A. silvestrii* and *A. amblyops,* but has the clypeal teeth in a distinctive pattern. In all three of these species, four subequal truncate teeth occur between a pair of larger "corner teeth," which may themselves be more or less subdivided. In *silvestrii* and *amblyops,* the four middle teeth are more or less separate and autonomous, but in *luzonica* they are grouped into two partially fused pairs, one pair on each side of the midline. The frontal lobes are very close together, though not completely contiguous, so that this species is intermediate between the "*Fulakora*" and "*Stigmatomma*" groups in this respect. The worker of *luzonica* has the palpi segmented 4,3. Apparently this is the common small *Amblyopone* of the Philippines.

A. silvestrii has the four middle teeth very regular, equal in size, and close-set, separated by a wide gap on each side from the blunt, bipartite corner tooth. This gap is absent or weakly developed in *amblyops,* according to Karawajew's figure. *A. silvestrii* also has a densely punctate and more or less opaque alitrunk (petiole and postpetiole subopaque); the sculpture may not be quite so dense in *amblyops;* in *silvestrii,* the propodeal declivity is finely transversely striolate or shagreened, whereas in *amblyops* it is said to be "very smooth and shining."

[12] A group of species, related to *A. denticulatum,* from Europe, the Near East and North Africa, has workers medium to small in size, with very small eyes and reduced pigmentation in the worker. All of these species have the frontal lobes separated, if only narrowly so, and the clypeal apron normally has 5 truncate teeth, all socketed on tubercles, between the large "corner teeth;" the latter often bipartite. Santschi (1915) gives a reasonable key to the known species of the Mediterranean area. In *A. denticulata* the palpi are segmented 4,3.

The variety of *denticulata* called *gracilicornis* is only a small variant common in the Balkans and the Aegean region; I have seen the series in the Finzi Collection [MCZ] mentioned in the original description by Menozzi. I agree with Emery (1916) that *gheorghieffi* is only the male of *denticulatum.*

It seems likely that *A. santschii,* from Senegal, belongs with the *denticulatum* group, although the description is too sketchy to make this certain.

Dr. Kenneth Christiansen has given me some interesting small yellowish males with light brown heads, which he took in July and August, 1952 and 1953, in NW Tripoli Province, Lebanon, at 1100 m. altitude, and below the Turkish border, Latakia, Syria, at 800 m.; presumably both collections were made at light. These may be the males of an undescribed *Amblyopone* or of one of the species known from workers in North Africa.

[13] The variation, distribution and synonymy of *A. australis* and its close relatives has been discussed by Wheeler (1927: 1-20), Brown (1958b: 13-15) and Wilson (1958a: 142-143). *A. australis* shows strong geographical variation in several characters, some of which can be summarized in brief.

Sculpture of dorsum of head. In samples from southwestern and southeastern Australia, the longitudinal costulation of the front of the head usually extends only to near the level of the eyes or a little beyond. In New South Wales and Queensland the costulation varies widely by locality. A large proportion of the samples from the subtropical forests of northeastern New South Wales and southeastern Queensland have the costulation very extensive, reaching well beyond the eyes and often extending almost to the posterior cephalic border. This is also the condition in the Lord Howe and Norfolk Island populations, and in the New Zealand lots; presumably these populations represent historical introductions from eastern Australia. In samples from northern Queensland and New Guinea, the costulation is well developed, but does not usually extend very far beyond the eye; at least, it is distinctly shorter than in the southeastern Queensland samples. In southwestern Australia the costulae and punctures tend to be much coarser ("race *foveolata*") than elsewhere, but samples I collected in South Australia (Kangaroo Island — Kingscote, Rocky River and Ravine des Casoars; Lofty Range—Aldgate; Northern Flinders Ranges—Wilpena Pound) approach the Western Australian material in this respect, and make transition to the Victorian samples. Series from Tasmania, south central Victoria and the Australian Alps tend to have both the costulae and the punctures reduced.

Sculpture of mandibles. In southwestern Australia, South Australia, Tasmania, Victoria and the Alps generally, the dorsal and lateral surfaces of the mandibles are normally completely and regularly coarsely longitudinally striate. New Hebridean specimens are mostly of this type. In eastern New South Wales, one notes that some samples show a weakening of the striation along the external margin of the mandible, and in series from the New South Wales-Queensland border (National Park), many specimens have almost entirely smooth and shining mandibles, with scattered punctures. These may occur together in the same nests with specimens having nearly or quite completely striate dorsal and lateral mandibular surfaces. Such specimens look much like the sibling species *A. michaelseni*, which has predominantly smooth mandibles, and some of them further converge toward *michaelseni* in having the head slightly longer than broad and the genal tooth small in size. This extreme intranidal variation more or less matches the extensive variation in cephalic sculpture of the same series.

Farther north in Queensland, one finds a more consistent progression from largely striate to almost wholly smooth mandibles, the latter type prevailing in northern Queensland and New Guinea. The Lord Howe-Norfolk Island-New Zealand populations are of the intermediate type, with mandibles predominantly striate, but tending to be smooth along the outer borders.

Color. Pigmentation is difficult to evaluate in insects having as long a callow period as this species has, but the abundant material available does indicate some broad trends. In general, populations from most forested areas in southwestern Australia, Tasmania, Victoria, and the mountains of New South Wales have more or less reddish workers, although associated females may be much darker. However, in intermediate areas that are drier or without many trees, such as the western districts of Victoria, Kangaroo Island, and the Lofty and Flinders Ranges of South Australia, the workers are usually dark brown. In New South Wales and southern Queensland the color darkens, and most workers from Queensland, as well as all the mature individuals of New Guinea, Lord Howe, Norfolk Island and New Zealand, are dark brown or piceous, with lighter appendages. The New Hebrides series are intermediate on the reddish side. Some series

taken from rotten logs in wet forests near Melbourne (Dandenong Range) are uniformly very light, and more yellowish than red. Most red series come from beneath stones. In Queensland, where nearly all *australis* come from rotten logs, the prevailing color is dark brown.

Size. The workers show extreme size variation, even at single localities or within single nest series. The only trend that I can see in the available material is one toward a wider spread of variation on the mainland of Australia, particularly in the southeastern areas. Perhaps much of this variation is phenotypic in origin.

Other characters: There is considerable variation in the mandibular dentition, but it is in large part "random" and difficult to analyze. New Guinea specimens often tend to form a blunt tooth between the two largest teeth, and in Australia there may be one, two or even three teeth basad of the largest tooth; however, these always decrease in size toward the mandibular insertions. Variation in compound eye size is partly regional, partly allometric. Even in the smallest workers, however, there are 12-15 or more facets backed by pigment, and usually more than 20. In the New Zealand ("*cephalotes*") populations, the second and third funicular segments are unusually slender, but can be matched more or less closely by samples from eastern New South Wales.

Without detailing other variation in minor characters, I think it can be seen that variation in this species, whether individual or geographical, shows a high degree of discordance among the different character-systems. Certainly a character-by-character analysis in this case shows up the essential lack of a realistic basis for the old system of "races" and "varieties," which is here discarded. Aside from the possibility of cryptic allopatric species, always a consideration to be respected in wide-ranging forms, *A. australis* looks in its totality like one species.

The two obscure forms *A. michaelseni* and *A. leai* appear to be peripheral siblings of *A. australis* now undergoing displacement pressure from *A. australis* after an expansion of this species into their respective ranges.

As might be expected from elementary considerations of character displacement (see Brown and Wilson, 1956), *A. australis* shows the maximum amount of difference from each

of the siblings where it overlaps their respective ranges. Outside the zone of sympatry, *australis* sometimes displays some characteristics of the siblings, e.g., the very smooth mandibles of many Queensland *australis,* away from the range of *A. michaelseni,* which has predominantly smooth mandibles.

A. michaelseni was described from southwestern Australia, and I have seen a topotypic specimen collected there (Jarrahdale, J. Clark leg.). Clark also recorded samples from Victoria and New South Wales, but I have never seen any *michaelseni* from these eastern states, despite intensive collecting in Victoria and the close examination of several hundred nests of what all proved to be *australis.* Wheeler saw a specimen from Lucindale, South Australia. Apparently *michaelseni* is very rare and local, especially in the southeast, and its similarity in the field to *australis* makes it hard to spot. It has a slightly longer head than *australis,* the eyes are smaller (15 facets or less, not or scarcely pigmented), the genal teeth are completely lacking, and the costulae and punctures are much reduced.

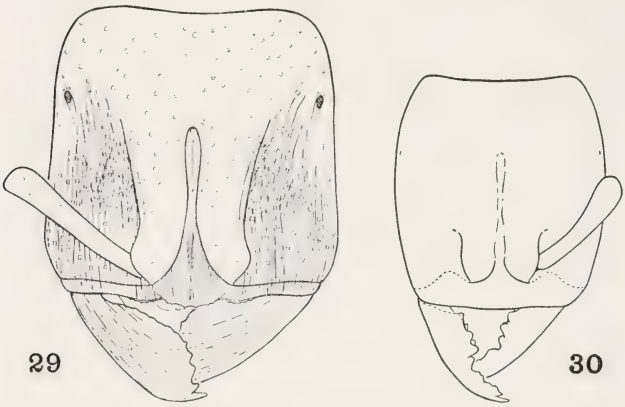
The Lord Howe sibling, *A. lcai,* is known from two series from the island, of which I have seen three syntype workers from the summit of Mt. Gervis. As compared to the *australis* (*"howensis"*) populations from the same island, the *lcai* sample is reddish-yellow in color (vs. dark reddish-brown), has smaller eyes with fewer and coarser facets (11-12 pigmented facets vs. 18-25), has short cephalic costulation, not or barely reaching beyond the eyes (vs. reaching nearly to posterior border), has slender second and third funicular segments (vs. segments II and III nearly or quite as broad as long), and has two well-developed subequal teeth basad of the large median mandibular tooth, while the latter tooth and its large distal neighbor are rather close together (vs. one distinct tooth basad of large median tooth, with sometimes an indistinct denticle basad of this; two large median teeth of mandible widely separated). It would be most interesting to investigate the relationship between these two species on Lord Howe, if they both still exist there.

[14] AMBLYOPONE MERCOVICHI sp. nov.
(Figs. 29, 32)

Holotype worker: TL 11.0, HL 2.04, HW 1.92 (CI 94), WL 2.98, petiole L 0.95, petiole W 1.11, scape L 1.12, exposed

straightline L of mandible 1.19 mm. In general size, color and shape of body resembling at first glance *A. australis* samples from the Victorian Alps, but with entirely different mandibles and other divergent characters.

Head as shown in Figure 29. Cheeks shallowly impressed in region outside frontal carinae and anterior to compound eyes. Eyes much reduced, with 6-7 facets in greatest diameter. Frontal



Two new species of *Amblyopone* from Australia, heads in full-face view. Figure 29. *A. mercovichi,* paratype worker. Figure 30. *A. gingivalis,* holotype worker. Drawn to same scale.

lobes broad, nearly horizontal, separated by a narrow median groove. Clypeus with a short but distinct median lobe, its apex rounded and denticulate, slightly overhanging the ventral or free clypeal border, which is also denticulate and is weakly concave in the middle. Genal angles rounded, unarmed. Labrum with the usual bilobed free margin, but also having a prominent transverse, bilobate ridge or welt near its middle, half of which is shown in Figure 29 as the stippled area below the clypeal margin. Mandibles subtriangular, much broader than those of

other *Amblyopone* species, the apical (masticatory) margin curving evenly into the basal margin. Apical margin with 5 distinct teeth, the apical largest, size of teeth decreasing basad; in approximate region of basal angle, the teeth are continued as a series of 5-6 low rounded teeth or crenulations passing onto the basal margin. The teeth and crenulations are single-ranked along the thin free inner mandibular margins.

Antennal scapes slightly incrassate apically, almost straight in dorsal view, but strongly curved to fit the genal curvature; when extended back, just barely reaching the compound eyes. Funiculi gradually incrassate toward apex, but without a distinct club; funicular segment II (counting pedicel as I) small, distinctly broader than long, the segments gradually increasing in length apicad to X, which is slightly longer than broad. Apical segment (XI) approximately twice as long as X. None of the specimens has the under-mouthparts opened out, but the apical segments of the maxillary palpi are visible in two specimens; this segment is flattened, curved and apically tapered; its length and position suggest that it is one of two segments in the maxillary palpus. The labial palpus is not visible, indicating that it is short and probably not more than 2-segmented.

Alitrunk rather narrow, with horizontal dorsal surface; anterior face of pronotum and sides of alitrunk steep; inferior pronotal angles acutely pointed. Alitruncal profile horizontal; pronotum and propodeum weakly convex (nearly plane), mesonotum weakly convex; metanotal groove distinct and impressed, with the slightly elevated mesonotum breaking an otherwise nearly straight alitruncal profile. Mesonotum from above subcircular, slightly broader than long, its boundaries distinct; constriction of alitrunk distinct, centered at metanotum; sides of propodeum diverging slightly caudad. Declivity of propodeum steep, flat, on each side with a low, rounded margin. Petiolar node with vertical, concave anterior face, meeting the almost flat (gently convex from side to side) dorsal face at an acutely rounded angle (Fig. 32).

Postpetiole a little shorter than the (normally exposed and pilosity-bearing part of the) succeeding segment, abdominal IV. Terminal segment of gaster conical, not compressed.

Body and appendages chiefly smooth and shining, with numerous piligerous punctures over upper part of head, dorsum of

alitrunk, sides of pronotum, petiole, postpetiole (where strongest and most numerous) and abdominal segment IV. The cheeks anterior to the eyes, the gula, and the mandibles are rather coarsely longitudinally striate, with coarse interspersed punctures. Median lobe of clypeus more finely striate. Sides of posterior alitrunk finely striolate-punctate, chiefly longitudinally. Anterior coxae shagreened subopaque.

Most surfaces of body, especially gaster and dorsal surfaces elsewhere, with a thin pubescence of rather coarse, short, reclinate hairs. Longer, more erect tapered hairs, mostly on anterior dorsum of head and clypeus, masticatory and ventrolateral borders of mandibles, gula, antennae, and apical and ventral parts of gaster; also a few of these longer hairs on pronotum and fore coxae.

Color rich ferruginous red; slightly infuscate spot on vertex.

The holotype, with three paratype workers, was taken by Father C. Mercovich at Kinglake West (="Tommy's Hut"), Victoria, on November 15, 1951. The four workers were taken from the heart rot of a large, rather dry eucalypt log lying on the forest floor. One of the workers was found in what appeared to be the ants' midden, containing large numbers of heads of termites, which may possibly therefore have been a main item of food. In this connection, it is interesting to note that *A. mercovichi* bears certain resemblances to presumed cryptic termite-predators in other ant groups (e.g., *Cylindromyrmex* Mayr, *Metapone* Forel, *Gnamptogenys* of the *mordax* group).

This large and curious ant, although it occurs in country near Melbourne, is known only from the type collection. Father Mercovich's finds, in this and the case of *A. gingivalis* sp. nov. (below) prove that even the relatively well-collected parts of Australia hold many a surprise for the enterprising and persistent collector.

A. mercovichi is so different from all other *Amblyopone* known that it almost warrants being placed in a new genus. Still, its affinities with the *australis* and *saundersi* groups seem clear enough, despite the aberrant mandibles. We need to know more about this species.

The holotype and 2 paratypes (one with no head) have been returned to Father Mercovich for deposit in an Australian collection. (Smallest paratype: TL 9.3, HL 1.80, HW 1.72 (CI 96),

WL 2.64, petiole L 0.83, petiole W 0.95, scape L 1.02, exposed straightline L mandible 1.05 mm.). One paratype in MCZ.

[15] AMBLYOPONE GINGIVALIS sp. nov.
(Figs. 30, 31)

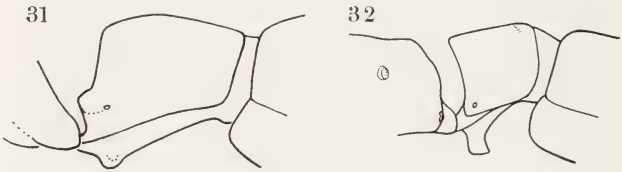
This new species is known from a single worker collected by Father C. Mercovich, S.J., at Calga, New South Wales, during April, 1956. Father Mercovich sent me the specimen together with the sample of *A. mercovichi*, described as new above, and Mrs. Buffler prepared figures of the head (Fig. 30) and petiole (Fig. 31) under my supervision. I then returned these specimens to Father Mercovich in Australia, after which, learning of my progressing revision of the tribe, he very generously returned them to me so that I might present the description with the rest of the material on the amblyoponines. Unfortunately, the shipment suffered damage in transit, and the sole worker of *gingivalis* lost its entire head and the anterior part of the prothorax. It might seem wiser to forego description of a unique holotype missing its most important parts, but in this case we do have a good drawing of the head available, and the species is of such particular interest in connection with the limits of variation within the genus, that I have decided to give it a name.

Holotype worker: TL 8.6 (estimated), HL 1.5 (estimated), HW 1.4 (estimated) (CI 91 from drawing); WL 2.1 (estimated), petiole L 0.82, petiole W 0.68 mm. Estimated straightline L of mandible 0.9 mm. Form of head shown in drawing. Note extremely reduced eyes and clypeal apron, the latter completely unarmed, and the subtriangular mandibles, with fairly distinct basal border and mostly blunt teeth, partly double-ranked. Scapes short, subclavate; genal angles unarmed.

Remainder of body typically amblyoponine in form, slender; alitrunk constricted at metanotum (seen from above). Mesonotum nearly three times as broad as long, bounded behind by a distinct, shallowly impressed metanotal groove. Alitruncal dorsum in profile horizontal; promesonotum and propodeal dorsum forming separate feeble convexities. Propodeal declivity sloping caudad, forming on obtuse angle with the dorsum, into which it is gently rounded. Petiolar node longer than high and longer

than broad (Fig. 31). Postpetiole nearly as long as the succeeding segment; last visible segment (abdom. VII) laterally compressed; extruded sting very long, slender, curved.

Sculpture of head (as recalled) densely and finely punctate or reticulate-punctate and predominantly opaque. Alitrunk, petiole and gaster mainly smooth and shining, with sparse punctures. Sides of alitrunk and anterior sides of petiole finely striate with scattered punctures, the striae principally longitudinal. Body overall with numerous fine, short, obliquely erect hairs and smaller, reclinate, pubescence-like hairs, not obscuring the sculpture. Color medium reddish-brown, head more brownish, appendages lighter.



Two new species of *Amblyopone* from Australia, petioles and adjacent parts in side view. Figure 31. *A. gingivalis*, holotype worker. Figure 32. *A. mercovichi* paratype worker. Not drawn to same scale.

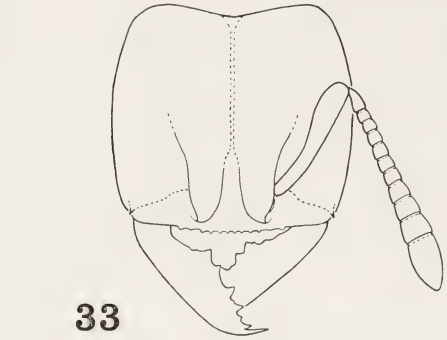
This species is so distinct in the shape of its clypeus and mandibles that there should be no chance of confusing it with any other *Amblyopone*. Undoubtedly it is a specialized relict, probably local in distribution. Father Mercovich took the sole worker under a stone in a gully with *Angophora* and scribbly gum (*Eucalyptus haemastoma*) trees as cover. The holotype will be returned to Father Mercovich for deposit in one of the Australian collections.

[16] The *ferruginea* group as presently known includes five Australian species: *aberrans*, *clarki*, *ferruginea*, *hackeri* and *longidens*, the first two of which are southwestern and the last three southeastern. The workers of all are stoutly built, small-eyed, yellow forms, smaller than *A. australis* and relatives, but not much different in general habitus. In fact, the *ferruginea*

group occupies a position intermediate between the *saundersi* and *australis* groups in size, structure and presumably in biology, and may well represent the descendants of the line that led from *saundersi*-like ancestors to *A. australis*. Like both contiguous groups the members of the *ferruginea* group have a palpal formula of 2,2 in the workers, while the clypeal apron, its dentition, and the male-female wing venation are reduced as in *australis*. The females, where known, are distinctly larger than the workers and have the head, alitrunk and petiole more or less dark brown or blackish. The males are smaller and blackish. The species are all strongly cryptic in habits, and normally nest and forage below the soil surface, so that they are rarely seen except when flooding forces them to the surface, or in the cold of winter, when they may rise beneath stones to seek the heat stored there from solar radiation. There are no good observations known to me on nest size, behavior or food preferences, but I think that some colonies must attain a large size. Like many subterranean ants, members of this group are found in a great variety of habitats, including wet forest, alpine scrub, and arid woodland. The systematics of the group were partly clarified by Brown (1952), who showed that Clark's *mandibularis* was the same as *ferruginea* Smith (Fig. 36), and that *ferruginea* is a local species, so far found only in Melbourne and vicinity. Forel's variety *longidens* is really a good species (Fig. 34) (confused by Wheeler in 1927 with *ferruginea*), widespread but local in southeastern Australia.

A. hackeri (Fig. 39), the most "*Fulakora*-like" of the *ferruginea* group, occurs in the country on the border between southeastern Queensland and northeastern New South Wales. Portions of a dismembered chilopod were found in a nest of this species taken by P. F. Darlington in southeastern Queensland.

Of the southwestern forms, *aberrans* (Fig. 35) and *clarki* seem distinct enough in mandible type, despite the considerable variation in dentition shown by *clarki* (Figs. 33, 37, 38). In addition, samples having the general *clarki* habitus (Fig. 33) show unusually strong geographical variation in sculpture, which may in fact represent differences between two or even three separate species. Specimens from the type series (Ludlow, W. A.) (Fig. 37) and a series from Busselton, W. A. (J. Clark



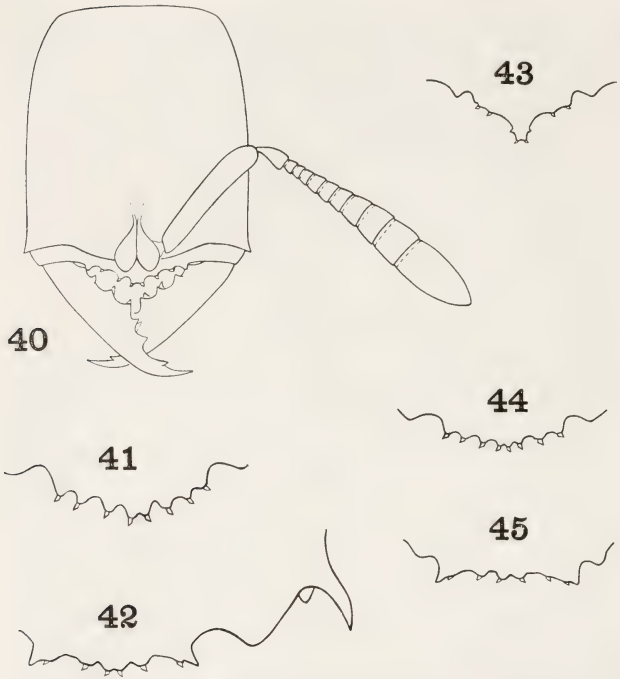
Australian *Amblyopone* of the *ferruginea* group, workers. Figure 33. *A. clarki* or near, Norseman, W. A., full-face view of head and mandibles. Figure 34. Right mandible and anterior clypeal margin, *A. longidens*, Grampians Range, Vict. Figure 35. Same, *A. aberrans* syntype, Mundaring, W. A. Figure 36. Same, *A. ferruginea*, specimen compared with type, Research, Vict. Figure 37. Same, *A. clarki* syntype, Ludlow, W. A. Figure 38. Same, *A. clarki* or near, Perth, W. A. Figure 39. Same, *A. hackeri* syntype, National Park, Queensland.

leg.) have the coarse, longitudinally striate or costulate sculpture of head and pronotum usual in species of the group. A worker taken by C. P. Haskins under a log in the National Park, W. A., of which the mandible and clypeal margin are shown in Figure 38, has the upper half of the head and the pronotum with numerous coarse, separated punctures in place of the costulae. Three workers (Fig. 33) taken by E. O. Wilson in arid woodland at Norseman, W. A. (which is far inland from the other *clarki* localities) have even more reduced sculpture; the punctures are much finer than in the National Park specimen, and the interspaces smooth and shining. More material is needed from southwestern Australia in order to clarify this situation.

[17] A number of small forms occurring in southeastern Australia and New Zealand are placed in the *saundersi* group. Already described as species are *exigua, wilsoni, lucida, punctulata* and *gracilis* from Australia, and *saundersi* from New Zealand. These forms all have the "*Fulakora* habitus;" i.e., they are small and slender, depigmented and with eyes much reduced or absent in the worker; the mandibles, clypeus and genal teeth are of the "typical *Stigmatomma*" pattern, and the lobes of the frontal carinae are fused or contiguous at the midline of the head. All have dense, fine punctate sculpture of the head. The palpi are apparently all segmented 2,2 (rarely 1,2).

It seems impossible for the time being to say how many good species there really are in this group. I am adding a new species that is quite distinct from any of the others (*A. smithi* sp. nov., described below). Only for *saundersi* do I have material from more than two or three localities, and this species is so variable that doubts must remain as to whether it may not represent two or more sibling species existing in New Zealand (Brown, 1958b).

There are differences among the species in head shape (especially CI), mandibular dentition, overall size and sculpture, but the best character is often the form and dentition of the anterior clypeal apron. In two series I have from Wallaby Creek in the Hume Range, central Victoria (D. Ashton leg.), and from Sherbrooke Forest in the Dandenong Range, Victoria (Brown leg.), the center of the clypeal apron is produced into



Australian *Amblyopone* of the *saundersi* group, workers. Figure 40. *A. smithi* sp. nov., paratype, full-face view of head. Figure 41. Anterior margin of clypeal apron, *A. gracilis* syntype. Figure 42. Same, *A.* sp. from Binna Burra, southeastern Queensland (left anterior corner of head with genal tooth also shown). Figure 43. Same, *A.* sp. from the Hume Range, central Victoria. Figure 44. Same, *A. exigua* from Kallista, Victoria, determined by Clark. Figure 45. Same, *A. lucida* syntype.

a definite median lobe (Fig. 43), while in paratypes of *A. lucida* from Coree (or Corrie) Creek in the Alps of the Capital Territory (G. Hill leg.) and a series from Bonang, Victoria, also in the eastern Alps (P. F. Darlington leg.), the apron is very nearly straight and has a differently arranged dentition (Fig. 45).

Most samples from Australia have clypeal aprons intermediate between these last two types (Figs. 41, 44). I have specimens of *exigua* Clark (Fig. 44), collected and determined by Clark himself, from Kallista, Victoria, which is adjacent to the type locality (Belgrave) and close to Ferntree Gully, where I collected another series of this same species. It should be noted here that Sherbrooke Forest, where the specimens (noted above) with the mesally lobate clypeal apron were found, is immediately adjacent to Belgrave and Kallista, and it seems likely that all of the specimens came from the same wet forest that clothes this limited area. That we are dealing here with a pair of sympatric species seems assured. Possibly the lobate form from Sherbrooke Forest and Wallaby Creek is an undescribed species, but since Clark's descriptions and figures are so vague, I cannot be sure that this form does not match his *A. wilsoni*, of which I have seen no authentic specimens.

Paratypes of *gracilis* (from Beech Forest on the Otway Peninsula of Victoria) are larger in size, but have a clypeal apron (Fig. 41) similar to that of *exigua*. A series matching the *gracilis* paratypes very well was taken by P. F. Darlington at Corinna, Tasmania. Another series taken by the same collector at Corinna is similar, but the insects are smaller in size; about half of them are ergatoid females with larger eyes.

This last collection agrees well with Clark's characterization of *punctulata*. In spite of their similarity, the two Corinna samples may belong to different species (*gracilis* and *punctulata*).

One more series, this from Binna Burra, near Beechmont in southeastern Queensland (P. F. Darlington leg.), is similar in size to *gracilis*, but has much larger genal teeth (Fig. 42), and the sides of the propodeum are largely smooth and shining (striolate, opaque in *gracilis, saundersi* and other similar species). Possibly this species is undescribed. It is clear that we need much more material of this group in order to be sure of the species.

Amblyopone smithi sp. nov.
(Fig. 40)

Holotype worker: TL 2.6, HL 0.56, HW 0.44 (CI 79), WL 0.69, petiole L 0.29, petiole W 0.29, scape L (without basal

neck) 0.26, exposed straightline L left mandible measured from lateral insertion 0.36 mm. Habitus of *saundersi* group, but much smaller than any of the other species known, and with *ca.* posterior 2/5 of the head distinctly shining, the punctures here coarse and numerous, but separated by predominantly smooth and shining interspaces; a median smooth strip extends forward to about the center of the head. The anterior half or slightly more of the head is densely punctulate, with intermixed indistinct longitudinal-oblique striolation, nearly or quite opaque.

The general shape of head, mandibles and antennae is shown in Figure 40. The eyes are reduced to minute, indistinct pigmented spots, each backing 2 or 3 indistinct facets. Mesonotum transverse, its posterior limits marked only by a feeble constriction; metanotal groove obsolete, a faint trace visible in certain lights. Propodeal dorsum meeting declivity through an obtuse, rounded angle; declivity plane, oblique, broader than high. Petiolar node sessile, a little longer than high; ventral process subquadrate, with rounded anterior corner and sharply rectangular posterior corner. Anterior face of node vertical, rounding into horizontal, weakly convex dorsum; seen from above, the node is approximately square, with rounded anterior corners. Postpetiole about as long as petiole, and only slightly wider; succeeding segment (abdominal IV) about as long as postpetiole, but slightly wider. Apex of gaster conical; sting stout, curved.

Sculpture, apart from head, predominantly smooth and shining, with scattered piligerous punctures. Lower mesepisterna and almost all of sides of propodeum, as well as mandibles, longitudinally striolate, but still moderately shining. Clypeus longitudinally striate. Pilosity as described for *A. monrosi*. Color ferruginous yellow.

Holotype [MCZ] and one very similar paratype worker [to be deposited in a major Australian collection] collected together from under a stone in clayey soil in dry eucalypt forest (predominantly *Eucalyptus Baxteri*, *E. obliqua* and *E. cosmophylla*) at Aldgate, near Mt. Lofty in the Lofty Ranges of South Australia, altitude about 550 m., December 8, 1950 (leg. W. L. Brown, Jr.). The weather at the time of collecting was very hot and dry; much digging turned up no further specimens.

This species is named for my long-time friend and adviser in myrmecology, Dr. Marion R. Smith.

[18] *A. celata* is a small yellow species, widespread in the Solomons. I was able to count only the maxillary palpal segments: there are four. Mann found that the pupae are naked, as in myrmicines. Apparently this species is replaced on New Guinea by *Prionopelta.*

[19] *A. zwaluwenburgi* is a minute species (under 2 mm. total length) that was found in the soil of a sugar cane field at the Hawaiian Sugar Planters Association Experiment Station, Honolulu. I think it is likely that the species has been introduced into Hawaii from Melanesia or the East Indies.

[20] Wilson (1958a) has discussed the variation of *Myopopone castanea* in some detail, emphasizing the Melanesian populations. He has synonymized five of the species, all described by Donisthorpe from 1938 to 1949, and there is every reason to accept his synonymy. Wilson's study extended only incidentally to the more western populations of *M. castanea,* which fall outside Melanesia proper, and it is now possible to study these in the light of additional material from the Philippines and elsewhere. Most of this material is included in the collection of Dr. J. W. Chapman, and comes principally from the vicinity of Dumaguete on Negros, Leyte, Palawan and southern Luzon (collected by Chapman, Baker, Williams, Brues and McGregor). Other material comes from northern Borneo (Mjöberg), Sumatra (Brues), etc.

The varieties *bakeri* Viehmeyer and *proxima* Stitz are represented by type material in the Museum of Comparative Zoology: comparison of these with the rest of the Philippine series shows that they are both part of the intraspecific variation of the *castanea* of that area. The characters of sculpture, and especially the shape of the subpetiolar process, show wide variation overlapping that of the New Guinea-Solomons samples.

The females, which are even more variable than the workers in sculptural characters, and which differ considerably from the workers of the same series, have been a source of synonymy

even dating back beyond Donisthorpe's time. Bingham described *moelleri* from Sikkimese examples taken at light, and Stitz added a variety *striatifrons* based on females from Lombok and western Sumatra; the latter were compared only with Bingham's very sketchy description. Neither description mentions any features outside the usual variation of the sample of *castanea* in the Museum of Comparative Zoology.

Roger described *M. rufula* from Batjan, thinking even then that it was "perhaps only a local variety" of *M. maculata*, described from Ceylon; later (1863, Verzeichniss der Formiciden Arten und Gattungen, Berlin, p. 20) he synonymized *rufula* with Smith's *castanea*. Probably the *rufula* and *castanea* types came from the same series collected on Batjan. Emery (1911) considered *maculata* to be a subspecies of *castanea*, which is more in line with the present conception of geographical and individual nest variation within a single species. Since we know that the "diagnostic" characters of these forms vary discordantly among themselves, there seems little reason to recognize a Ceylonese or a more widespread variant under a formal name. The variety *bugnioni* Forel, described from Ceylon, was never satisfactorily separated from *maculata*, and is undoubtedly the same geographical variant.

There remains only *Myopopone beccarii* Emery, described from worker material from Ternate. According to the original description, *M. beccarii* is supposed to differ from *M. castanea* chiefly in having the mesonotum and petiole longitudinally rugulose and subopaque. In view of his qualifying remarks following the diagnosis, it seems that Emery may have meant "metanotum" instead of "mesonotum." A sample of workers from central Cape York Peninsula, Queensland, has faint striation or longitudinal rugulation between the coarse punctures of the propodeum (="metanotum") and petiolar dorsum, and the striation of the sides extends farther up onto the dorsum than in many other *castanea* samples. It seems that this may represent an approach to the condition Emery found in *beccarii*. In any case, *beccarii* comes from the middle of the range of *castanea*, and it seems unlikely that it is more than an extreme sculptural variant of the latter. Emery himself apparently lost some confidence in the distinctness of *beccarii*, because his Genera Insectorum entry (1911) rates *beccarii* as a mere subspecies of

castanea, along with *moelleri* and *maculata.* Wilson (1958a) made no attempt to evaluate *beccarii,* and recognized it provisionally as a species only on the basis of the original description and grounds of virtual sympatry with *castanea.* Although I have not myself examined the types, I feel that the study of the variation in both eastern and western populations of *castanea* reveals sculptural extremes that are probably about as aberrant as described by Emery for *beccarii,* and I therefore consider that *beccarii* should be placed provisionally in the synonymy of *castanea.*

I have listed below the synonyms of *M. castanea* in chronological order. In those cases where the date is enclosed in parenthesis, Wilson (1958a: 144) has already given the full reference in indicating the synonymy, and the details will accordingly be omitted here. (T) before the entry indicates that either Wilson or myself has reviewed type material.

(T) *castanea* (Fr. Smith) (1860).
maculata Roger, 1861:50, worker, female. Type loc.: Ceylon. N. syn.
rufula Roger, 1861:52, worker. Type loc.: Batjan. Syn. Roger, 1863.
beccarii Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, (2)4:447, worker. Type loc.: Ternate. N. syn.
moelleri Bingham, 1903:34, female. Type loc.: Sikkim, 7000 ft. N. syn.
bugnioni Forel, 1913, Zool. Jahrb. Syst., 36:5, nota, worker, female, male. Type loc.: Peradeniya, Ceylon. N. syn.
(T) *bakeri* Viehmeyer, 1916, Ent. Mitt., 5:283, worker. Type loc.: Tacloban, Leyte, P. I. N. syn.
(T) *proxima* Stitz, 1925, Sitzb. Ges. naturf. Freunde, Berlin, 1923, p. 110, *nomen nudum;* descr. Wilson, 1958a:145. N. syn.
striatifrons Stitz, 1925, Sitzb. Ges. naturf. Freunde, Berlin, 1923, p. 110, female. Type locs.: Lombok and w. Sumatra. N. syn.
(T) *picea* Donisthorpe (1938)
(T) *wollastoni* Donisthorpe (1942)
smithi Donisthorpe (1946)
(T) *rossi* Donisthorpe (1947)
(T) *similis* Donisthorpe (1949)

[21] The species-level taxonomy of the Neotropical *Prionopelta* has been much confused. Mayr described the holotype female of *P. punctulata* as having 11 antennal segments. In his generic diagnosis of 1911, Emery noted that *Prionopelta* (so far as he personally was acquainted with the species) had 12 antennal

segments in worker and female, and he felt that Mayr had been misled by an "anomaly." But material now available proves that southeastern Brazil and northern Argentina are inhabited by a species having 11 segments and corresponding reasonably well to Mayr's description of the type female and his later (1887) description to the worker. This species, which I consider to be *P. punctulata,* varies somewhat both inter- and intranidally in size, strength of sculpture, and intensity of the yellow pigment. Forel, utilizing differences he supposed to exist on the basis of a comparison of Mayr's two (female and worker) descriptions, gave the name *mayri* to the worker from Santa Catarina. The differences cited are in minor sculptural and pilosity features, and it seems best to accept Mayr's original opinion that his worker and female belong to the same species, rather than Forel's judgment based on the descriptions. Santschi described *P. bruchi* in 1923 from Alta Gracia, Córdoba, Argentina, apparently from the worker caste, although the description is headed by the symbol " ♀ " — probably a typographical error. Santschi's description is in the form of a comparison with "*mayri,*" although he does not state how he verified the determination of the *mayri* specimens used for the comparison. The differences mentioned are minor ones, subject for the most part to differences of viewing angle and interpretation, as well as to allometric variation. Santschi does not give a count of the antennal segmentation, the most important diagnostic character in this case. Samples taken since in Argentina by Kusnezov and others are all 11-segmented and appear to represent a single species, which I refer to *P. punctulata.* I myself have seen workers and males from Tucumán, Argentina (N. Kusnezov, P. Wygodzinsky leg.), and from Loreto, Misiones, Argentina (A. Ogloblin leg.). Kusnezov has determined the males from Tucumán as *bruchi.* It seems to me that there is no reason any longer to doubt the synonymy of *bruchi* with *punctulata.* Two workers from Agudos, S. Paulo, Brazil (W. W. Kempf leg.) belong to this species also.

Two other Neotropical *Prionopelta* species have already been eliminated from consideration: *P. mocsaryi* Forel, supposedly from Paraguay, appears to be a mislabeled sample of the Melanesian *P. opaca* Emery (Wilson, 1958a:149); *P. marthae*

Forel is a synonym of *Typhlomyrmex rogenhoferi* Mayr, according to Brown, 1953a.

All of the other forms of *Prionopelta* from the Americas have 12-segmented antennae in worker and female. They may be divided on the basis of cephalic sculpture into two groups. One kind corresponds to the first lug of couplet 2 in the short key below; this is the clearcut species *P. modesta,* with coarsely punctulate and opaque head. E. O. Wilson collected it at Las Hamacas, 17 km. north of Santiago Tuxtla, Veracruz, and at Pueblo Nuevo, near Tetzonapa, in the same state. At both localities, it was a common ant in the leaf litter of tropical evergreen forest; notes on the ecology and behavior of this species are given below. Other samples of *modesta* in the Museum of Comparative Zoology come from Finca El Real, Ocosingo Valley, Chiapas (C. and M. Goodnight and L. J. Stannard leg.), and from the vicinity of Guatemala City in orchid plants intercepted by U. S. Plant Quarantine at San Francisco. A series from Barro Colorado Island, Panama Canal Zone (J. Zetek leg.) is the only sample of *modesta* known from outside the Guatemala-southern Mexico area.

The remainder of the twelve-segmented forms, including types of the two nominal species *antillana* and *amabilis*, form a rather heterogeneous lot. The *antillana* type (St. Vincent, B. W. I.) in the Museum of Comparative Zoology has the anterior clypeal margin projecting somewhat forward and bluntly subangulate in the middle, and the cephalic sculpture is weak and subopaque, with sparsely punctulate, smooth and shining areas just mesad of the eyes. Specimens from Tumupasa, in the Amazon watershed of Bolivia (W. M. Mann leg.) agree well with the *antillana* type. Other series from Colombia, Costa Rica, Honduras, Guatemala, and even (one worker) Pueblo Nuevo, Veracruz, are very variable in cephalic sculpture, ranging from sparsely punctulate and shining to densely but very indistinctly punctulate and subopaque. In some of these specimens, the anterior clypeal margin can be seen, and is gently and evenly rounded; in other cases the anterior clypeal margin cannot be seen satisfactorily because the mandibles have not been opened. The relationship of *antillana* to *amabilis* remains obscure as far as I am concerned; much more material will be needed to decide the variation and limits of these two species.

The present distinctions among the American *Prionopelta* species are summarized in the following key to the workers and females:

Key to Neotropical species of Prionopelta based primarily on workers

1. Antennae 11-segmented (n. Argentina, se. Brazil) .... *punctulata* Mayr
   Antennae 12-segmented ..... 2.

2. Punctulation of head coarse, uniform over entire dorsum, deep and densely arranged, rendering the whole surface nearly or quite opaque (s. Mexico, common; C. America) ..... *modesta* Forel
   Punctulation of dorsum of head fine and shallow, often varying in distinctness and density from area to area; either spaced, with smooth, shining intervals, or combined in an indefinite, subopaque roughening of the surface (s. Mexico, C. America) ..... *amabilis* Borgmeier
   (Lesser Antilles, Bolivia, ?C. America) ..... *antillana* Forel

[22] A colony of *P. modesta*, taken at Pueblo Nuevo, Veracruz, by E. O. Wilson, was studied for several weeks in a glass-topped plaster nest in the laboratory. The colony contained eggs, which hatched in the laboratory, but the dealate female apparently was not fertilized, and was not the colony queen. At the time of capture, other females were found in the colony with wings, as also in other colonies found at the same locality (August, 1953). The colonies often appear to be split into sections separated more or less from one another, and occupying small bits of rotting wood or bark in the leaf litter. Some of the fragments contain only workers, or workers and larvae, indicating that the colonies may be very loosely organized (like those of *Amblyopone*) and more or less nomadic.

Newly hatched larvae in the laboratory nest spent much time raising and moving about the anterior part of the body, possibly an activity functioning to attract workers with food. Several attempts were made to get the *Prionopelta* workers to accept various kinds of live and dead arthropods, but the workers are exceedingly timid foragers, and almost always recoiled violently when their antennae came into contact with the potential prey. Even such delicate animals as live *Tomocerus* (Collembola) and fresh-killed *Drosophila* adults were treated in this way by the ants. After repeated contacts within a very cramped foraging

chamber, the ants finally killed a partly-grown geophilomorph centipede about 15 mm. in length — that is, much longer than the ants, which are about 2 mm. long. The ants grasped the centipede by a leg with a very rapid lunge of body and mandibular closure too quick to be observed in detail, and immediately doubled up and attempted to sting in the leg joints or body of the centipede. The centipede showed obvious agitation each time it was stung, and raced about, doubling and redoubling its body until the ant was finally dislodged. After being stung, the centipede showed impairment of locomotor activity of the segments behind the point where the ant had been attached, and ran rather crookedly, but after a few minutes showed partial recovery. Discontinuous observations covered several more individual attacks by different ants, and the following day, the ants were found to have removed the centipede, now motionless and apparently dead, to the brood chamber, where some larvae were now attached and feeding. Other later trials with small centipedes were made at a time when the colony was in its final stages of disintegration, and the ants simply fled upon the slightest movement of the centipedes.

The general impression gained from these observations was that *P. modesta* is capable of biting, hanging onto, and stinging into immobility even relatively large arthropods (such as a geophilomorph of the size indicated), but that such large prey animals would not normally be available in circumstances of confinement allowing the *Prionopelta* to attack them. Especially is this indicated when one considers that the usual result of physical contact between centipede and ant was the hasty retreat of both. Perhaps the usual prey will be found to include even smaller, juvenal centipedes or symphylans; search of the nests should be made to determine what *Prionopelta* feeds upon.

[23] The *Prionopelta* of the Old World occur in Madagascar, southeastern Africa and the Indo-Australian region. The Madagascan species (*descarpentriesi*) and the one from the mainland of Africa (*aethiopica*) are both known from single collections. They have not been compared directly with each other or with most other species of the genus, and the characters separating them as species are not clear from the descriptions. Since I

have seen no material from these regions, I am merely placing the two names in the list as species without judging them further.

In the Indo-Australian region there are four nominal species, of which *brocha,* isolated on New Caledonia, is a very distinct relict (Fig. 15). The other three species are *majuscula* (New Guinea), *opaca* (New Guinea) and *kraepelini* (Java). *P. majuscula* and its synonymy have been discussed by Brown (1953b) and Wilson (1958a). So far as known, it is confined to northern New Guinea. It has moderately punctate, shining workers, yellowish in color and somewhat larger than *kraepelini* and *opaca* workers. Its females are distinctly larger than its own workers, and are a contrasting dark brown in color.

In *kraepelini* and *opaca,* the queens are scarcely larger than the workers and tend to have similar sculpture and color if from the same nest or locality. I have now seen a great deal of new material of these two forms, and the distinction between them is becoming blurred. Together, they turn out to have a vast range, from northern Queensland (at least) in the southeast to Java and the Philippines to the west and north. The typical *opaca* come chiefly from New Guinea and parts of Micronesia. They are usually brownish in color and have coarse, dense punctation over the body from head onto the first gastric segment at least. Workers and females of *kraepelini* usually have much less dense punctation, and the alitrunk and gaster are predominantly smooth and shining. I have seen samples more or less closely agreeing with *kraepelini* from several Micronesian localities; from Buitenzorg, Java (the *kraepelini* type locality); from Dumaguete, Negros, and Mt. Makiling, Luzon in the Philippines (J. W. Chapman Coll.); and from Mt. Bartle Frere, 1000-1600 m. (P. J. and P. F. Darlington leg.) and the Elliot Range, *ca.* 1000 m., near Townsville (Darlingtons leg.) in Queensland. Father J. J. McAreavey also sent me a couple of workers of this species which, he wrote me, came from the Grampians Range in western Victoria. I questioned this range at the time (which was before the Queensland records were available), but Father McAreavey has assured me (*in. litt.*) that the Grampians record is not based on a labelling error. Still, the Grampians record remains so astonishingly far beyond the other localities that only further collections there will remove all doubts about a possible

mixup. The specimens are very similar to some in the Museum of Comparative Zoology from Dumaguete in the Philippines. Perhaps in favor of the Grampians record is the fact that the two Queensland collections both came from rather high levels on mountains.

In Micronesia, there are found forms intergradient between *opaca* and *kraepelini*. While I have not studied the Micronesian material at any length, I believe that probably most of the *kraepelini* specimens really are only smoother, light-colored variants of *opaca*, situated peripherally to New Guinea. It is interesting to note that the workers of *majuscula* have the smooth integument and light color approached by *kraepelini* outside New Guinea; many extra-New Guinea workers also appear to be more robust, in this tending toward *majuscula*. Apparently we have in *opaca* another case of centrifugal variation based on New Guinea, and involving character displacement against the parapatric species *majuscula*.

The relationship of *kraepelini* to *opaca* needs to be reviewed with more and better material than I now have before me. Also to be considered is the relationship of these species to the neotropical species; the *kraepelini* topotypes, although not well-preserved, are rather smooth and unusually pale, and do resemble *P. antillana*. It is not beyond possibility that this population may have reached Buitenzorg from the New World in plantings for the Botanical Gardens there. The Dumaguete samples were taken in an "Old Cemetery," and this and other circumstances suggest strongly that *Prionopelta* species like this one are often transferred accidentally by human commerce.

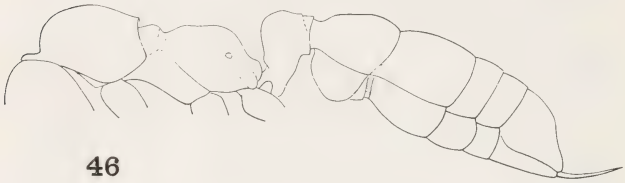
*Key to Indo-Australian species of Prionopelta, based primarily on workers**

1. Genal teeth well developed and acute (Fig. 15), more than 0.02 mm. long; size larger, head width of holotype worker 0.64 mm. (New Caledonia) *brocha* Wilson

   Genal teeth minute to obsolete, never more than 0.01 mm. long; smaller spp., head width not exceeding 0.55 mm. in worker ..... 2.

**Dorylozelus mjoebergi* Forel, from Queensland, may possibly be a *Prionopelta*. It is supposed to have only 11 antennal segments, which should separate it from the species in the key, all 12-segmented.

2. Size larger; head width $>$ 0.47 mm. in worker; worker feebly sculptured, shining, yellowish in color; female distinctly larger than worker, dark brown (New Guinea) ..... *majuscula* Emery
Size smaller; head width $<$ 0.47 mm. in worker; color pale yellow to brown; female nearly same color and size as workers from same nest; sculpture variable, but always coarse on New Guinea (e. Australia, New Guinea, Micronesia, Java, Philippines)
opaca Emery and *kraepelini* Forel



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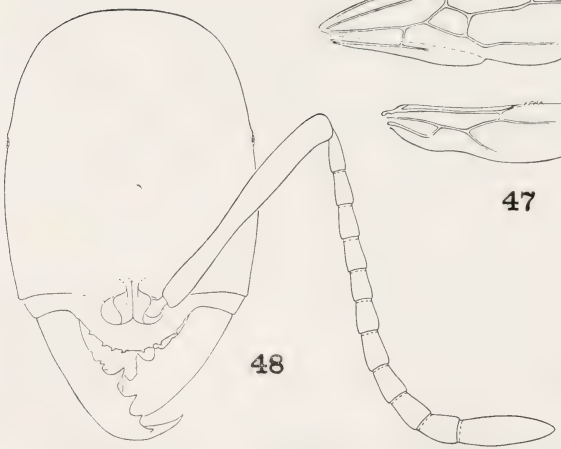

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Onychomyrmex. Figure 46. *O. hedleyi*, worker, outline of body from side view. Figure 47. Male wings, probably *O. mjoebergi*, specimen from the National Park, southeastern Queensland. Figure 48. *O. hedleyi* worker, full-face view of head.

[24] The known ranges of the three *Onychomyrmex* species have been increased in eastern Queensland in recent years, mainly through the activities of P. J. Darlington, Jr. (PJD) in 1932 and 1957-1958, and his son, P. F. Darlington (PFD) in 1957-1958. I (WLB) made a few collections in northern Queensland in 1950.

O. doddi: western slope of the Macalister Range, east of the Black Mountain Road running north from Kuranda, about 100 workers in a small rotten log in rain forest (WLB). This is only a few miles from Kuranda, the type locality.

O. mjoebergi: Mt. Spec Plateau, 2000-3000 feet altitude, about 40 miles north of Townsville (PFD). National Park, in McPherson Range, on the southern border of Queensland, 3000-4000 feet (PJD); workers and males were taken separately. The petiole of the workers from southern Queensland differs slightly from that of northern samples, but not enough to convince me that they are separate species.

O. hedleyi: Mt. Bellenden Ker, east side, 3000-4500 feet (PJD). Mt. Spec Plateau, 2000-3000 feet (PFD). Malanda, 2200 feet (WLB). Kuranda, 1100 feet (WLB). Mt. Spurgeon, 3500-4000 feet (PJD). Thornton Peak, near Daintree, 1000-4000 feet (PFD). Eungella Range, west of MacKay (PFD).

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the manuscript and added valuable biological observations, but this is not meant to imply their responsibility for any of the views expressed in this paper.

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Included here are names of ant species, genera and higher categories mentioned in the body of this paper. Names cited in the Appendix and captions to figures are excluded where reference is made to them through bracketed numbers at the primary (species-list) reference. The pages of the primary references are given in boldface below. Abbreviations for generic names are as follows: A. = Amblyopone, Myop. = Myopopone, Myst. = Mystrium, O. = Onychomyrmex, P. = Prionopelta.

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LAND SHELLS OF NAVASSA ISLAND, WEST INDIES

By Ruth D. Turner

With Seven Plates

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No. 5 — *Land Shells of Navassa Island, West Indies*

By Ruth D. Turner

No study of the mollusks of Navassa Island has been made since 1866 when only a few dead specimens were available. This paper is based on a large series of preserved material which has made it possible to determine the relationships of these mollusks to those of other islands in the West Indies.

Navassa is a small, isolated island located about 40 miles west of the Tiburon Peninsula of Haiti and about 85 miles northeast of Morant Point, Jamaica, at north latitude 18° 25′ west longitude 75° 05′. It is an elevated coral reef of about 1.5 square miles in extent, one and one-fourth miles at its longest point, and with an elevation of 250 feet at its highest point. It is pear-shaped in outline and in profile is said to look like a huge battleship with the lighthouse for a mast, or a gigantic straw hat with a low, flat crown. The island rises abruptly from fairly deep water, the depth at the shoreline averaging about 12 fathoms. On all except the north coast there is a deep undercut at the water level. The sea cliffs average about 40 feet in height above which there is a bench of some 100 yards in width and then a steep slope which leads to the rather flat crown. The width of the bench varies somewhat, being very narrow at the northwest point but widening gradually toward the south and east. The island is virtually inaccessible from the sea and today is 'boarded' by climbing a chain ladder which hangs from the cliffs at Lulu Bay on the lee side. The entire surface of the limestone island is pitted with holes varying from five to more than forty feet in depth and from a foot to several yards in diameter. As a result, though the island receives a fair rainfall, it is physiologically dry. There are no ponds and frequent drilling of wells has never produced any fresh water, for all rain water is rapidly drained off by the numerous fissures and caves. This type of terrain makes walking on the island most difficult and W. J. Clench (1930) wrote, "Most of our excursions consisted of a long series of jumps from the rim of one hole to that of another," and he says that it could take as long as four hours to walk a mile.

The island of Navassa was practically unknown until 1857 when Captain E. K. Cooper of Baltimore, Maryland, and Peter Duncan discovered the phosphatic guano deposits while making soundings around the island. They took possession of the uninhabited island and worked the deposits for a time before the formation in September 1864 of the Navassa Phosphate Company of New York, of which E. K. Cooper was a member of the executive council. The reports to the company in 1864 of Dr. G. A. Liebig, chemist, and Augustus H. Fick, mining engineer, gave an excellent picture of the rich phosphate deposits and of the condition of the the island at that time. In November 1865 Eugene Gaussoin, mining engineer and metallurgist, sailed from Baltimore on the company brig with the vice-president of the company and Peter Duncan, captain, to visit the island. The purpose of his visit was to advise the company on means of finding water, improving mining techniques, shipping facilities and other matters. In his report, he wrote that at that time there were "30 white men, officers and mechanics, and 180 black laborers" on the island and all food, water and other supplies had to be shipped in from great distances — a formidable task! However, the company was reasonably successful for a time, though working under great difficulties, but in 1898, during the Spanish-American war, the company failed and the island was abandoned. During World War I a detachment of marines was stationed there for a time. With the building of the Panama Canal, the amount of shipping through the Windward Passage increased greatly and it became most important to have a lighthouse on the island to protect shipping from this treacherous rock rising out of the sea. The lighthouse was completed in October 1917 and from that time until 1929, when the light was made automatic, the island was inhabited by the three families who attended the light. Again during World War II the island was garrisoned by American troops. Today, the island is uninhabited and is seldom visited except by members of the U.S. Coast Guard who service the light, and occasional hunters who go there to shoot wild goats — descendants of those left by the lighthouse keepers.

Though few biologists have ever visited the island, the flora and fauna are now quite well known and are remarkable for the

number of endemic species in several phyla which occur on such a small area. In December 1929, W. J. Clench visited the island and later wrote, "It is a bird island and thousands of boobies were nesting all over the place, in the small trees, on the low bushes and even among the low vegetation. A few frigate birds were also nesting and to see these beautiful birds close at hand was a royal experience." Wetmore and Swales (1931) listed 20 species of birds from Navassa of which one, the Navassa ground dove, is peculiar to the island.

In July 1917, R. H. Beck collected there for the American Museum of Natural History, and from this collection of reptiles K. P. Schmidt (1919, 1921) described a new genus and five new species of lizards, all endemic. He listed 13 species from the island and related them to species found in Jamaica, Hispaniola and Cuba. Cope (1886) described an iguana, probably collected by Gaussoin, but this large lizard has apparently been extinct for a long time; it was undoubtedly exterminated by the laborers working the phosphate deposits who would have used it for food. Proctor (1959) states that "no less than 10 endemic species of lizards have been reported."

In an excellent paper on the flora of Navassa Island, E. L. Ekman (1929) wrote, "needless to state, this vegetation, for all its freshness in the rainy season, is well suited to survive even the severest of droughts. The roots of the trees like the *Ficus* penetrate into the rock fissures to astonishing depths. The *Metopium* sheds, if necessary, all its leaves in winter. The savanna plants belong to different types of xerophytes . The cacti are succulents, the grasses and the sedges survive by means of their drought- and fire-resisting rhizomes, and the weeds defy the dry season here in the same way as they do the winter in the north. The unproportionately great number of annuals on Navassa, c. 30, or about 33 per cent of the total number of plants, bear mute witness to the efficacy of their means of protection." An interesting and rather surprising thing about the flora of Navassa is the almost complete lack of halophytes, for only two species can be classed as such. Ekman listed 102 species of vascular plants for the island, 44 of which are probably indigenous and 8 species and two varieties are endemic.

Only three species of land shells are known from this small island and these were all described by George Tryon in 1866. He had received a small series collected by Eugene Gaussoin, the mining engineer mentioned above. His collecting, however, was casual and all of the material was dead and worn. As a result, the systematic position and island relationship of these species have remained uncertain.

In December 1929 a Harvard University Expedition, led by William J. Clench accompanied by William E. Schevill and Harald A. Rehder, visited the island. They landed December 29, and spent two weeks of intensive collecting of all groups of plants and animals. This was during the dry season and the land shells were probably not as active as at other times so that it was necessary "to move and turn over several tons of rock before sufficient numbers were secured for study." A single pupillid was found the day they arrived while they were laboriously carrying their supplies up the steep slope to the lighthouse quarters where they were going to live. Not having a proper container available the minute specimen was placed in a match box and unfortunately it fell out and was lost. Continued intensive search failed to turn up another specimen. It is possible that collecting on the island during the rainy season might add to the known molluscan fauna. As a result of this collecting we are now able to show that two of the three species of land shells, all of which are endemic to the island, are related to species in Jamaica, one to Haiti.

Considering the unreceptive shores of Navassa, its undercut and precipitous rocky cliffs, it would be virtually impossible for any plant or animal, with the possible exception of lizards, to reach the island by rafting. Consequently, whatever the population (excluding those species introduced by man), it seems safe to conclude that the original species were carried there by hurricanes. The large number of endemic species on the island would suggest that it is old and has been isolated for a very long time. Versey (in Proctor, 1959), reporting on the Foraminifera, stated that "the micro-facies appear to be very similar to that encountered in the Pliocene Coastal Limestones of the North Coast of Jamaica. The only foraminifera present are Operculinoides and Heterostegina, both of which range from Eocene to Recent. The age of the limestone probably lies within the range Miocene-Recent."

It is also possible, of course, that these species have differentiated rapidly as may happen in small isolated populations. Whatever the factor involved — long isolation or rapid evolution — the molluscan species are all well differentiated.

Since Tryon had only a few dead and worn specimens at the time he described these species he could not give the range of variation nor even describe them completely. Consequently they are redescribed here.

Eutrochatella circumlineata Tryon

Plate 1, figs. 1-3; Plate 7, figs. 3-5

Helicina circumlineata Tryon 1866, American Journal of Conchology, vol. 2, p. 305, plate 20, fig. 13 (Navassa Island).

Description. Shell trochoid, reaching 11.5 mm. in height, solid, heavy, imperforate, pale ivory to salmon in color and sculptured with spiral cords. Whorls 6 and slightly convex. Suture slightly impressed. Spire conic and produced at an angle of about 77°. Columella short, nearly straight and curving into the basal lip. Aperture oval and cast at an angle of about 55° from the base. Outer lip simple, not reflected. Inner lip consisting of a thinly glazed area on the body whorl. Sculpture consisting of numerous, fine, evenly spaced spiral threads. There are about 32 on the body whorl, those above the periphery being slightly coarser and more widely spaced than those on the base. Color ranging from a pale ivory to salmon, the body whorl usually lighter in color than the earlier whorls. Parietal area and lip white. Interior of the aperture a medium to rather deep orange. Embryonic whorls 1¼, very small, smooth and white. Operculum subquadrate with a thin chitinous base and a well developed calcareous outer surface which has a thickened ridge on the parietal margin. Nucleus near the parietal margin, growth lines concentric. Color of the operculum ranging from orange to salmon, becoming lighter as the calcareous deposit thickens near the parietal margin.

height	width	
9	9.5 mm.	all adult specimens
10	11.5	
10.5	11.5	
11	11	

Types. The holotype is in the Academy of Natural Sciences, Philadelphia, from Navassa Island, collected by Mr. Eugene Gaussoin.

Remarks. Tryon described this species from two dead, bleached specimens and he did not see the operculum. The present series shows a variation in color from light ivory to salmon. The operculum is similar to that of other species placed in this genus and the radula fits well within the range of variation for the genus *Eutrochatella* as given by H. B. Baker (1922). However, it seems to combine the characters of his subgenus *Troschelviana* (type species *Helicina erythraea* Sowerby) and the subgenus *Eutrochatella* (type species, *Helicina pulchella* Gray). The lateral teeth of *E. circumlineata* have large, well developed cusps as in *erythraea* but the marginals are very numerous as in *pulchella*. In addition, the large fourth lateral (called the T-lateral by Baker) of *circumlineata* bears a number of well developed cusps as in *erythraea*. This tooth in the subgenus *Eutrochatella* as given by Baker is smooth or nearly so.

This species seems to be most closely related to *Eutrochatella costata* Sowerby from the vicinity of St. Ann's Bay, Jamaica, but differs in being considerably larger though less coarsely sculptured. The radulae of *circumlineata* and *costata* are also nearly identical, both species having numerous marginals and denticulate laterals.

In his field notes, Dr. Clench stated that *circumlineata* was found "mostly under stones and flat limestone slabs. They were found in quite barren areas under the top layer of loose flattish stones and were moderately abundant."

Chondropoma (Chondropoma) navassense Tryon

Plate 1, figs. 4-7; Plate 2; Plate 7, figs. 7-9

Chondropoma navassense Tryon 1866, American Journal of Conchology, vol. **2**, p. 305, pl. 20, fig. 12 (Navassa Island).

Chondropoma (Chondropoma) navassense Tryon. Henderson and Bartsch 1920, Proceedings United States National Museum, vol. **58**, p. 62.

Description. Shell reaching 20 mm. in length (truncated specimen) rather thin in structure but strong and finely sculptured. Spire extended, truncate except in very young specimens,

and produced at an angle of about 32°. Umbilicus small, extending to the embryonic whorls, and nearly covered by the reflected lip in adult specimens. Color a uniform dull yellowish brown. Interior of aperture a shiny yellow-brown, lip white. Whorls remaining 4 to 5, and moderately convex. Suture moderately impressed with, in some specimens, a shallow channel on the body whorl which increases slightly in width and depth toward the aperture. Aperture subcircular. Outer lip simple, very slightly reflected and with a small angular projection in the region of the anal canal. Inner lip narrow, simple, not appressed against the body whorl and partially covering the umbilicus. Axial sculpture consisting of numerous, fine, more or less evenly spaced ridges. Spiral sculpture consisting of evenly spaced threads of about the same strength giving a rather uniform reticulated pattern. Small nodules are produced where the ridges and threads cross. Umbilicus bordered by 3 or 4 prominent spiral cords. Operculum subcircular, paucispiral and with a thin granular calcareous deposit on the outer surface.

height	width	
20	20 mm.	adult, truncated specimen
15.5	10	" " "

Type. The holotype is in the Academy of Natural Sciences, Philadelphia, collected by Eugene Gaussoin. The type locality is Navassa Island. Paratype in the Museum of Comparative Zoology no. 78164, received from Mr. Tryon.

Remarks. The original description of this species was based upon five dead specimens; in fact, Tryon was not sure of the color of the shell and he did not see the operculum. To my knowledge no additional collections of this species were made until Navassa was visited by W. J. Clench, W. E. Schevill and H. A. Rehder in 1929-30. In his field notes Dr. Clench wrote that these snails were "most abundant under rocks, especially 200 to 300 feet N.W. of the lighthouse. They were quite abundant in the tufts or clumps of grass about the roots and adjacent edges of stones. On the S.E. side of the island many were found climbing trees to a height of 5 to 6 feet and aestivating in protected nooks about the roots or on the branches."

As a result of this collecting we are now able to figure the operculum and the radula in addition to gaining an understanding of the range of variation within the species. On the basis of the rather large series collected, this species appears to be remarkably uniform in color for this group, there being no evidence of any color pattern, and all specimens being a uniform yellowish brown. The variation in size and proportions is also within rather narrow limits, the greatest variation coming in the amount of truncation.

This species is probably most closely related to *Chondropoma* (*Chondropoma*) *brownianum* Weinland from Gonave Island, Haiti. However, it is readily differentiated by its uniform color, the striking but variable color pattern of *brownianum* consisting of axial bands of red brown on a pale buff ground color. These bands may be entire, interrupted or in the form of triangular spots, and the intensity of the color may also vary considerably. *Chondropoma* (*C.*) *molense* Bartsch from the Le Mole River on the northern peninsula of Haiti and *Chondropoma* (*C.*) *montalbense* Bartsch from Coteaux on the southern peninsula are also closely related. In fact, these last two species seem to be at best only subspecies of *brownianum*. The size, sculpture and shape of the aperture of all are very similar.

The radula of *navassense* shown in Plate 7, figure 9 is similar to that shown by Hidalgo (1947) for species in the related genus *Chondrothyra*, except that the denticles on the second laterals are well developed in *navassense* whereas on the second laterals of *Chondrothyra* the denticles are lacking entirely or are very small. The radula of *navassense* is almost identical to that shown by H. B. Baker (1924) for *Tudora*.

Chondropoma navassense feeds on the thin coating of grayish lichens on the bark of the bushes, trees and rocks. Their feeding tracks are shown, greatly enlarged, on Plate 2.

Zaphysema (Zaphysema) gaussoini Tryon

Plate 3, figs. 1-3; Plate 4; Plate 7, figs. 2, 6

Helix gaussoini Tryon 1866, American Journal of Conchology, vol. **2**, p. 304, pl. 20, fig. 11 (Navassa Island).

Helix (*Coryda*) *gaussoini* Tryon. Pilsbry 1889, Manual of Conchology, ser. 2, vol. **5**, p. 47.

Hemitrochus gaussoini Tryon. Pilsbry 1889, *ibid.*, ser. 2, vol. **5**, p. 197.
Cepolis (Dialeuca) gaussoini Tryon. Pilsbry 1895, *ibid.*, ser. 2, vol. **9**, p. 183.
Sagda gaussoini Tryon. Clench 1945. Mollusca, vol. **1**, no. 5, p. 65.

Description. Shell depressed-globose, reaching 11 mm. in greatest diameter, imperforate, smooth and a light straw-yellow in color. Whorls 5½, moderately convex and increasing rapidly, the body whorl being large and somewhat inflated. Suture moderately impressed. Spire depressed and produced at an angle of about 113°. Columella short, slightly thickened, curved and merging into the basal portion of the outer lip. Aperture oval and cast at an angle of 58° from the base. Outer lip thin, simple and not reflected. Inner lip consisting of a very thin glaze on the body whorl. Sculpture consisting only of indistinct growth ridges. Color of shell beneath the periostracum light ivory. Periostracum thin, a light straw-yellow in color and persistent. Columella area white. Embryonic whorls 1½, white, smooth and shining.

height	greatest diameter
9	11 mm.
8.5	10

Type. The holotype is in the Academy of Natural Sciences, Philadelphia, from Navassa Island, Mr. Eugene Gaussoin, collector.

Remarks. Tryon described this species from a single dead specimen, and in his original description related it to *Helix melanocephala* Gundlach from Cuba. Over the years its systematic position has been quite uncertain. As noted in the synonymy above, Pilsbry placed this species in three different groups all belonging in the family Fruticicolidae [Cepolidae]. Fortunately the Harvard Expedition found this species alive and collected a large series of them. They were carefully relaxed and preserved so that it has been possible to make a study of the anatomy and so determine its proper systematic position. There is now no question that *gaussoini* belongs in the family Sagdidae; W. J. Clench placed it in the genus *Sagda* on the basis of the shell texture and structure. A study of the reproductive anatomy has shown that it belongs to the genus *Zaphysema* which is also

in the Sagdidae but which until now was not known to occur outside of Jamaica. It was also fortunate that preserved specimens of *Z. tenerrima* C. B. Adams, the type species of *Zaphysema* Pilsbry, were available for dissection so that comparisons could be made and the figures of both could be published together. The lectotype of *Helix tenerrima* C. B. Adams is figured on Plate 3, figure 6.

The illustrations of the anatomy of the reproductive system of *Z. tenerrima* C. B. Adams from Jamaica given here differ somewhat from that given by Pilsbry (1892, pl. 13, fig. F). However, Pilsbry had only a single specimen and was never able to check his work. He later states that this was one of his first land shell dissections and he obviously was not satisfied with it. So far as I know no other figure of this species has been published. Fortunately, I was able to make dissections of five specimens in all stages of reproduction of which three stages are figured.

The anatomy of the reproductive system of *Z. gaussoini* is very close to that of *Z. tenerrima*. It differs mainly in having a proportionately very much larger penial appendix, in having only three lobes in the ovotestis, in having the penial retractor muscle inserted near the end of the epiphallus fairly close to the opening of the vas deferens rather than near the base as in *tenerrima*. In both species the middle portion of the spermathecal duct is swollen to form a secondary spermatheca. From its side near the apical end arises the slender duct leading to the spermatheca. The spermathecal retractor is inserted very close to the end of the secondary spermatheca. In its normal position the entire spermathecal complex is interwoven with the prostate, uterus, and free oviduct; the spermathecal sac lies at the base of the albumen gland and the retractor muscle is attached to the sheath of the gland. In young or non-breeding specimens the penial appendix lies above the entire visceral mass and can be clearly seen through the body wall when the mantle is removed. In specimens full of eggs or young snails the appendix is pushed inward and the greatly enlarged uterus comes to lie on top of it. In one of the specimens of *tenerrima* dissected, the uterus was distended with 53 fully developed eggs with white, calcareous shells. The specimen figured in Plate 6, figure 1 contained over

40 young. Most of the specimens of *gaussoini* dissected were apparently young and none had more than one egg in the uterus. All of them were aestivating at the time they were collected. It is probable that fertilization takes place before aestivation so that the young are developed in the uterus during the dry season, hatching immediately when the adults emerge and thus having the benefit of the entire rainy season for growth.

Three aestivating colonies of *gaussoini* were found, each containing from 60 to 120 specimens. They were 1½ to 2 feet below the surface under loosely piled rocks, and the specimens were clustered together forming irregular balls. To my knowledge such a habit has not been recorded for any other member of the Sagdidae.

On the basis of shell characters as well as anatomy, *Z. gaussoini* seems to be most closely related to *Z. tenerrima*, and the radulae of the two species as shown on Plate 7, figures 1 and 2 are very similar.

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PLATES

Plate 1

Figs. 1-3. *Eutrochatella circumlineata* Tryon, Navassa Island, West Indies (4 X).

Figs. 4-7. *Chondropoma navassense* Tryon, Navassa Island, West Indies. Fig. 5, Paratype, MCZ no. 90,010 (all 3 X).

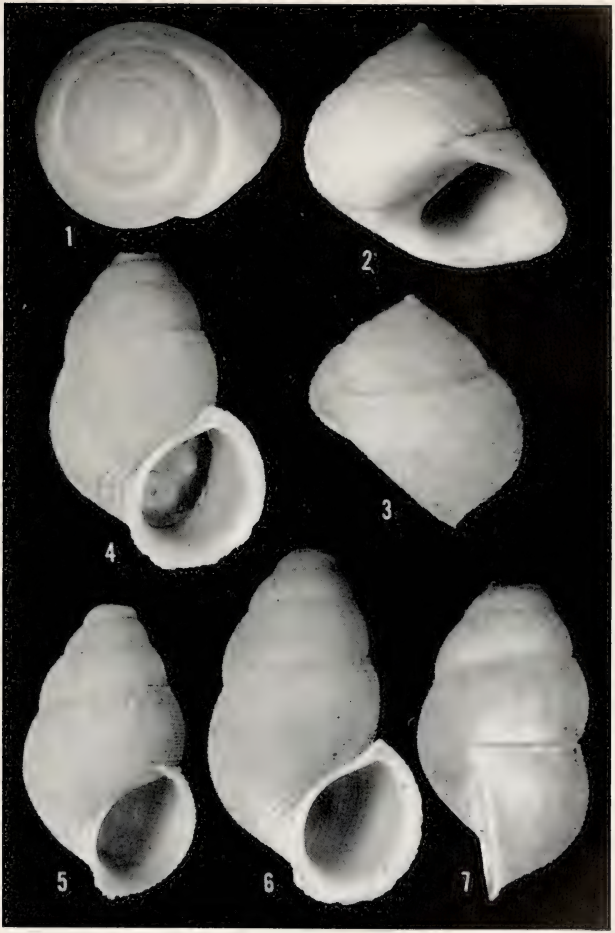


Plate 1

Plate 2

Feeding tracks of *Chondropoma navassense* Tryon (20 X).

In the area covered by this enlargement the snails were progressing from right to left in upward swinging tracks. When feeding the snail moves its head forward and upward, scraping off the whitish lichen, then moving its head slightly to one side, repeats the process so that it produces a small arc. Having reached as far as possible to the left and right it moves forward and clears another arc. A series of such arcs indicates the direction in which the snail was progressing. Each rectangular mark indicates a single sweep of the radula.

Plate 2

Plate 3

Figs. 1-3. *Zaphysema* (*Zaphysema*) *gaussoini* Tryon, Navassa Island, West Indies (3.5 X).

Figs. 4-6. *Zaphysema* (*Zaphysema*) *tenerrima* C. B. Adams. Jamaica. Fig. 6, Lectotype of *Helix tenerrima* C. B. Adams, MCZ no. 222184 (all 2 X).

Plate 3

Plate 4

Zaphysema gaussoini Tryon

Fig. 1. Anatomy of the reproductive system of an adult specimen (with a fully developed lip on the shell) at the beginning of egg production. The appendix has been stretched out slightly to show the basal portion. A single large egg can be seen in the uterus.

Fig. 2. Anatomy of an immature specimen in non-breeding condition to show differences in the proportions and shape of the various organs as compared with the adult. The appendix is in its normal position.

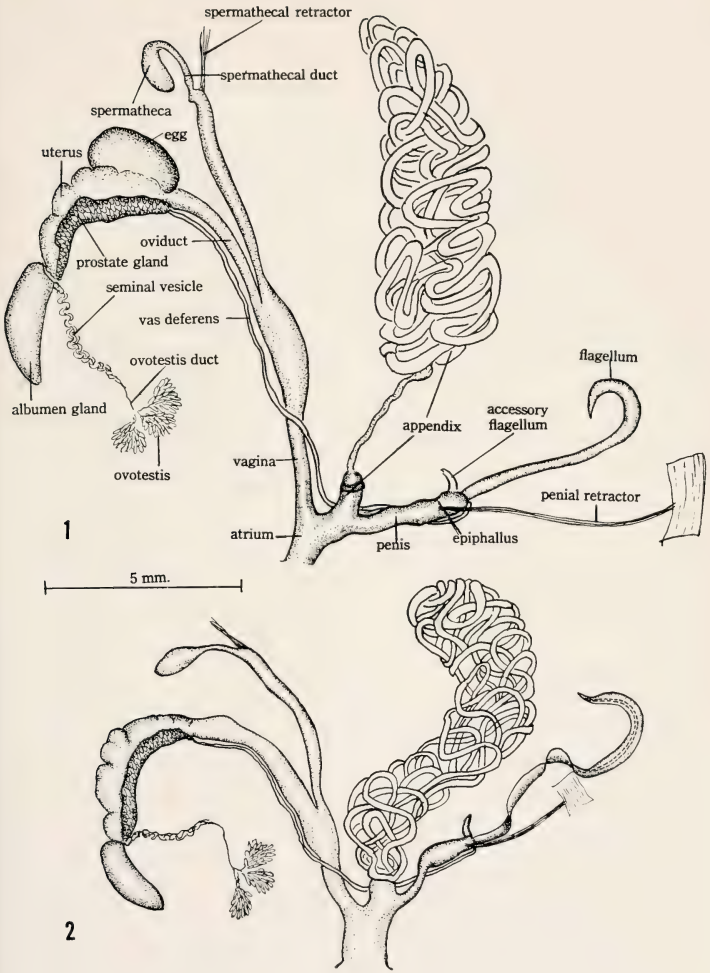

spermathecal retractor
spermathecal duct
spermatheca
egg
uterus
oviduct
prostate gland
seminal vesicle
vas deferens
ovotestis duct
albumen gland
ovotestis
vagina
atrium
penis
appendix
accessory flagellum
flagellum
epiphallus
penial retractor
1
5 mm.
2

Plate 4

Plate 5

Zaphysema tenerrima C. B. Adams

Fig. 1. Anatomy of the reproductive system of an adult specimen. The uterus was filled with eggs most of which fell out before the drawing could be made. There was a total of 53 eggs in the uterus of this specimen. The vas deferens was broken during the dissection. The appendix was flattened beneath the enlarged uterus. The prostate gland appears small in proportion to the greatly enlarged uterus. In all specimens of this species dissected the coiled portion of the appendix did not cover the basal portion. The spermatheca is collapsed.

Fig. 2. Anatomy of the reproductive system of an immature, non-breeding specimen. The ovotestis unfortunately could not be dissected. The prostate at this stage is nearly as large as the uterus and the spermatheca nearly circular in cross-section.

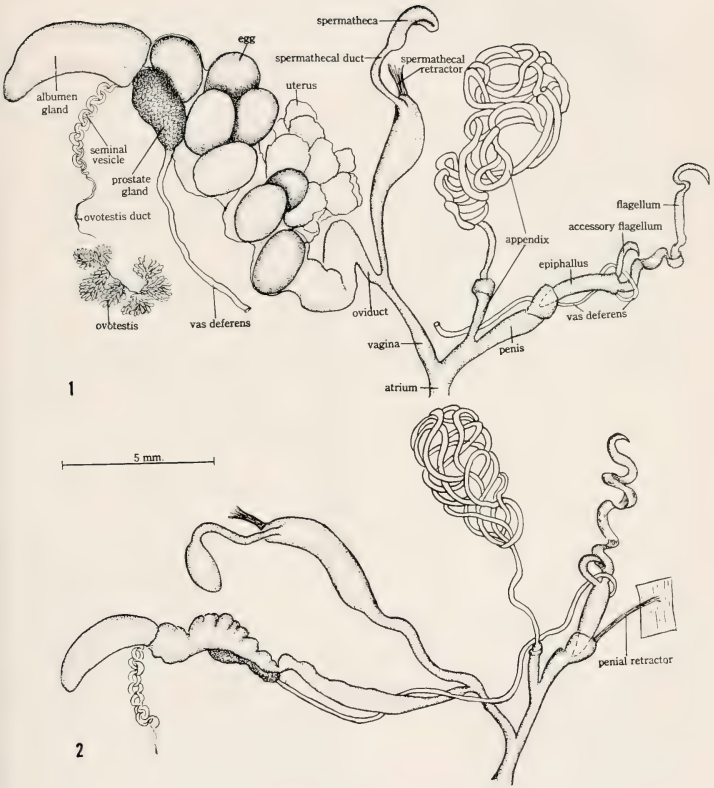

spermatheca
egg
spermathecal duct
spermathecal retractor
uterus
albumen gland
seminal vesicle
prostate gland
ovotestis duct
ovotestis
vas deferens
oviduct
vagina
atrium
penis
appendix
epiphallus
flagellum
accessory flagellum
vas deferens
1
5 mm.
penial retractor
2

Plate 5

Plate 6

Zaphysema tenerrima C. B. Adams

Fig. 1. A specimen with fully developed young ready to emerge. The drawing was made after the removal of the shell and the anterior portion of the mantle which forms the pulmonary cavity.

Figs. 2-3. Shells of *Zaphysema tenerrima* at the time of hatching.

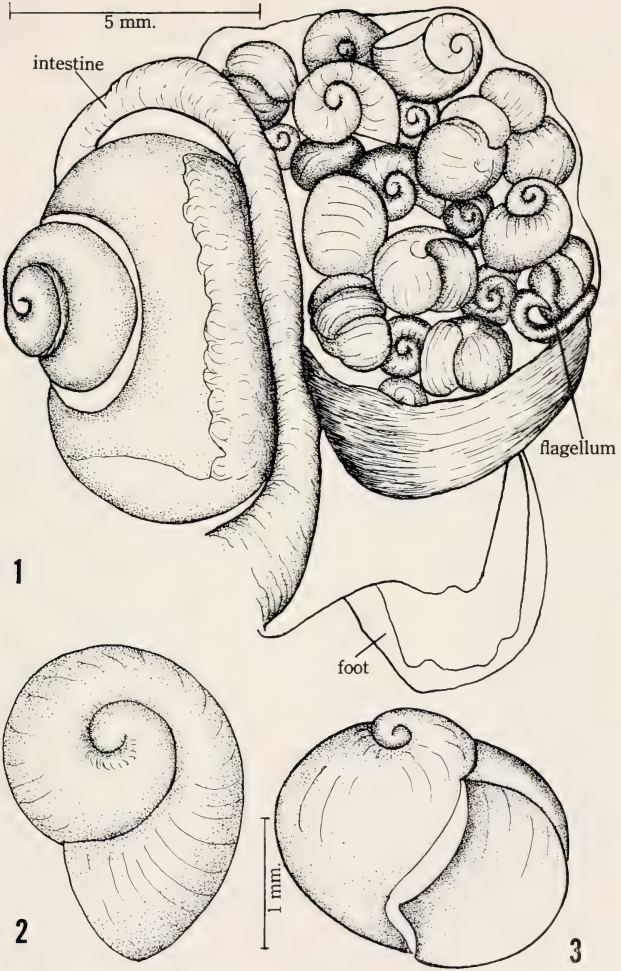


Plate 6

Plate 7

Fig. 1. Radula of *Zaphysema tenerrima* C. B. Adams.

Fig. 2. Radula of *Zaphysema gaussoini* Tryon.

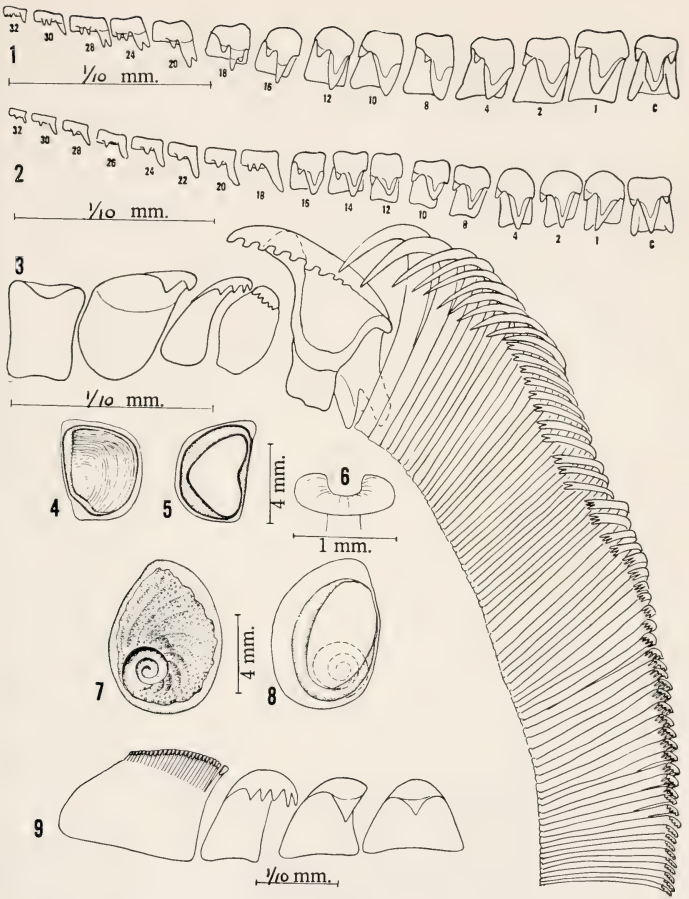
Fig. 3. Radula of *Eutrochatella circumlineata* Tryon.

Figs. 4-5. Operculum of *Eutrochatella circumlineata* Tryon. Fig. 4, outer surface. Fig. 5, inner surface.

Fig. 6. Jaw of *Zaphysema gaussoini* Tryon.

Figs. 7-8. Operculum of *Chondropoma navassense* Tryon. Fig. 7, outer surface. Fig. 8, inner surface.

Fig. 9. Radula of *Chondropoma navassense* Tryon.


1
32
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1/10 mm.
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5
4 mm.
6
1 mm.
7
4 mm.
8
9
1/10 mm.

Plate 7

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 122, No. 6

A TRANSCRIPTION OF DARWIN'S FIRST NOTEBOOK ON "TRANSMUTATION OF SPECIES"

Edited by

PAUL H. BARRETT
Michigan State University

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM

April, 1960

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WITH THE
MUSEUM OF COMPARATIVE ZOOLOGY
AT HARVARD COLLEGE

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PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 6 — *A Transcription of Darwin's First Notebook on "Transmutation of Species"*

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PAUL H. BARRETT
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FOREWORD

From July 1837 until July 1839, Darwin filled a number of notebooks on the subject of evolution. Six of these notebooks are now kept among the Darwin Papers at the University Library, Cambridge, England. The library has catalogued these books as follows:

INDEX TO MSS OF CHARLES DARWIN

Volume	Contents
121	"B" Notebook dealing with evolution theory. (10 x 17 cm.)
122	"C" Notebook dealing with evolution theory. February-July 1838. (10x17cm.)
123	"D" Notebook dealing with evolution theory. "July 15th 1838, finished October 2nd." (10x17cm.)
124	"E" Notebook dealing with evolution theory. "Finished July 10th 1839." (10x17cm.)
125	"M" Notebook dealing with evolution theory. "July 15th 1838." "This book full of metaphysics on morals and speculations on expression." (10x17cm.)
126	"N" Notebook dealing with evolution theory. Begun October 2nd 1838. "Metaphysics and expression." (10x17cm.)

Through the courtesy and assistance of Sir Charles G. Darwin, the University Library of Cambridge, and the All University Research Committee of Michigan State University, microfilmed

* Department of Natural Science, Contribution 143.

copies of these notebooks were made available to the present editor. A transcription of the first notebook "B" has been made and is presented herein. In making the transcription, Darwin's text has been reproduced as faithfully as possible, although punctuation has been added where necessary. In his rough notes, Darwin often did not use any punctuation at all and used capital letters indiscriminately. Since he wrote in his most hasty and elliptical style, some words at first were illegible. After reading the collateral works of Darwin and other authors of the period, and through the very generous and invaluable assistance of Sir Charles Darwin, Dr. Mary Alice Burmester of Michigan State University, and Dr. Sydney Smith of Cambridge University, it became possible to transcribe the obscure and illegible words. In some instances I have inserted articles, etc., to complete sentences or to correct grammar; such words are enclosed in square brackets, e.g., [the]. All words or phrases that Darwin enclosed in parentheses or scrawled between lines as afterthoughts, I have put in parentheses.

Most bibliographic references cited by Darwin in the notebooks were incomplete. These have been traced, and are included in the appended notes in their completed form. I have purposely kept editorial annotations and amendments to a minimum, seeking to leave unprejudiced the integrity, arrangement and completeness of the original notes insofar as possible.

There were originally 280 numbered pages in this notebook, of which 63 were later cut out by Darwin when he began writing *The Origin of Species*. Wherever pages are missing from the notebook, a notation has been inserted in the appropriate place in the text.

Excerpts from this notebook have been published previously in: *The Life and Letters of Charles Darwin*, 2 vols., New York, 1897, edited by Francis Darwin; *Darwin and the Darwinian Revolution*, Garden City, New York, 1959, by Gertrude Himmelfarb, and From Darwin's Unpublished Notebooks, *Centennial Review of Arts and Science*, Vol. 3, No. 4, Fall, 1959, East Lansing, Michigan, by Paul H. Barrett.

Grateful acknowledgments are due to Sir Charles Darwin and Lady Nora Barlow who kindly granted permission to edit and publish transcriptions of these notebooks.

[Transmutation of Species]
B [Notebook]
C. Darwin

(All useful pages cut out December 7, 1856, and again looked through April 21, 1873. This book was commenced about July, 1837. Page 235 was written in January 1838. Probably ended in beginning of February.)

ZOONOMIA

Two kinds of generation [i.e., reproduction]: the coeval kind, all individuals absolutely similar, for instance fruit trees, probably polypi, gemmiparous propagation, bisection of Planaria, etc., etc.; the ordinary kind, which is a longer process, the new individual passing through several stages (typical or shortened repetition of what the original molecule has done?). This appears highest office in organization (especially in lower animals, where mind, and therefore relation to other life, has not come into play); see Zoonomia[1] arguments; [reproduction] fails in hybrids where everything else is perfect; mothers apparently only born to breed, annuals rendered perennial, etc., etc. (Yet Eunuch, nor cut stallion, nor nuns are longer lived.)

Why is life short? Why such high object generation? We *know* world subject to cycle of change, temperature and all circumstances which influence living beings. We see the young of living beings become permanently changed or subject to variety, according to circumstances, [e.g.,] seeds of plants sown in rich soil, many kinds are produced, though new individuals produced by buds are constant; hence we see generation here seems a means to vary, or adaptation. Again we believe (know) in course of generation even mind and instinct become influenced. Child of savage not civilized man. Birds rendered wild through generation acquire ideas ditto. V. [i.e., *Vide*] Zoonomia.

There may be unknown difficulty with *full grown* individual with fixed organization thus being modified; therefore generation to adapt and alter the race to *changing* world. On other hand, generation destroys the effect of accidental injuries, which if animals lived forever, would be endless (that is, with our present systems of body and universe); therefore final cause of life.

With this tendency to vary by generation, why are species are [*sic*] constant over whole country? Beautiful law of intermarriages (separating) partaking of characters of both parents, and then *infinite* in number. In man it has been said, there is instinct for opposites to like each other. Ægyptian cats and dogs, ibis, same as formerly, but separate a pair and place them on a fresh [i.e., geologically new] island. It is very doubtful whether they would remain constant. Is it not said that marrying in *deteriorates* a race; that is, alters it from some end which is good for man? Let a pair be introduced and increase slowly, [safe] from many enemies, so as often to intermarry; who will dare say what result? According to this view animals on separate islands ought to become different if kept long enough apart with slightly differing circumstances. Now [e.g.,] Galapagos Tortoises, Mocking birds, Falkland Fox, Chiloe fox, English and Irish Hare.

As we thus believe species vary, in changing climate, we ought to find representative species; this we do in South America (closely approaching), but as they inosculate, we must suppose the change is effected at once, something like a variety produced (every grade in that case surely is not produced?). (Granting) species according to Lamarck[2] disappear as collections made perfect; truer even than in Lamarck's time. Gray's[3] remark, best known species (as some common land shells) most difficult to separate. Every character continues to vanish: bones, instinct, etc., etc., etc.

Nonfertility of hybridity, etc., etc.

If species (1) may be derived from form (2), etc., then (remembering Lyell's[4] arguments of transportal) island near continent might have some species same as nearest land, which were late arrivals; others old ones (of which none of same kind had in interval arrived) might have grown altered. Hence the type would be of the continent, though species all different. In cases as Galapagos and Juan Fernandez, when continent of Pacific existed, might have been monsoons, when they ceased, importation ceased, and changes commenced; or intermediate land existed, or they may represent some large country long separated.

On this idea of propagation [i.e., evolution] of species we can see why a form peculiar to continents, all bred in from one

parent; why Megatheria several species in S. America; why 2 of ostriches in S. America. This is answer to Decandoelle [*sic*][5] (his argument applies only to hybridity), genera being usually peculiar to same country; different genera, different countries.

Propagation explains why modern animals same type as extinct, which is law almost proved. We can see why structure is common is common [*sic*] in certain countries when we can hardly believe necessary, but if it was necessary to one forefather, the result would be as it is. Hence Antelopes at C. of Good Hope, Marsupials at Australia. (Will this apply to whole organic kingdom when our planet first cooled?) Countries longest separated greatest differences; if separated from immense ages[6] possibly two distinct types, but each having its representatives, as in Australia. This presupposes time when no Mammalia existed; Australian Mamm. were produced from propagation from different set, as the rest of the world.

This view supposes that in course of ages, and therefore changes, every animal has tendency to change. This difficult to prove, [e.g.] cats, etc., from Egypt. No answer because time short and no great change has happened. I look at two ostriches as strong argument of possibility of such change; as we see them in space, so might they in time. As I have before said, *isolate* species, especially with some change, probably vary quicker.

Unknown causes of change. Volcanic Island? Electricity.

Each species changes. Does it progress?

Man gains ideas.

The simplest cannot help becoming more complicated; and if we look to first origin, then must be progress. If we suppose monads are constantly formed, would they not be pretty similar over whole world under similar climates, and as far as world has been uniform at former epochs? How is this Ehrenberg?[7] Every successive animal is branching upwards, different type of organization improving, as Owen[8] says, simplest coming in and most perfect and others occasionally dying out; for instance, secondary terebratula may have propagated recent terebratula, but Megatherium nothing. We may look at Megatherium, Armadillos and sloths as all offsprings of some still older type, some of the branches dying out.

With this tendency to change (and to multiplication when isolated) requires deaths of species to keep numbers of forms equable; (but is there any reason for supposing numbers of forms equable? — this being due to subdivisions and amount of differences, so forms would be about equally numerous). Changes not result of will of animal, but law of adaptation as much as acid and alkali.

Organized beings represent a tree *irregularly branched,* some branches far more branched; hence Genera. As many terminal buds dying as new ones generated. There is nothing stranger in death of species than individuals.

If we suppose monad definite existence, as we may suppose in this case, their creation being dependent on definite laws, then

[Fig. 1]

those which have changed most (owing to the accident of positions) must in each state of existence have shortest life. Hence shortness of life of Mammalia.

Would there not be a triple branching in the tree of life owing to three elements — air, land and water, and the endeavour of each typical class to extend his domain into the other domains, and subdivision three more — double arrangement? If each main stem of the tree is adapted for these three elements, there will be certainly points of affinity in each branch. A species as soon as once formed by separation or change in part of country [has] repugnance to intermarriage; [that] settles it. We need not think that fish and penguin really pass into each other (?).

The tree of life should perhaps be called the coral of life, base of branches dead, so that passages cannot be seen. This again offers contradiction to constant succession of germs in progress (no, only makes it excessively complicated). [Fig. 1.]

Is it thus fish can be traced right down to simple organization, birds not? [Fig. 2.]

We may fancy according to shortness of life of species that in perfection, the bottom of branches deader, so that in Mammalia, birds, it would only appear like circles, and insects amongst articulata; but in lower classes perhaps a more linear arrangement. How is it that then come aberant [*sic*] species in each genus (with well characterized parts belonging to each) approaching another? Petrels have divided themselves into many

[Fig. 2]

species, so have the Awks [*sic*], then is particular circumstances to which . . .[9] Is it an index of the point whence two favourable points of organization commenced branching?

As all the species of some genera have died, have they all one determinate life dependent on germs, that germ upon another? Whole class would die out, therefore . . .[10]

In island neighbouring [a] continent where some species have passed over, and where other species have "air" of that place, will it be said, those have been then created there? Are not all our British Shrews diff[erent] species from the continent? Look over Bell[11] and L. Jenyns.[12]

Falkland rabbit may perhaps be instance of domesticated animals having effected a change which the Fr[ench] naturalists thought was species.

Study Lesson[13] Voyage of Coquille.

Dr. Smith[14] says he is certain that when White men and Hottentots or Negros [*sic*] cross at C. of Good Hope the children

cannot be made intermediate. The first children partake more of the mother, the later ones of the father. (Is not this owing to each copulation producing its effect, as when bitches puppies are less purely bred owing to having once born mongrels?) He has thus seen the black blood come out from the grandfather (when the mother was nearly quite white) in the two first children. How is this in West Indies? Humboldt,[15] New Spain.

Dr. Smith always urges the distinct locality or metropolis of every species; believes in repugnance in crossing of species in wild state.

No doubt (C.D.) wild men do not cross readily, distinctness of tribes in T. del Fuego; the existence of whiter tribes in centre of S. America shows this. Is there a tendency in plant's hybrids to go back? If so, man and plants together would establish Law, as above stated. No one can doubt that less trifling differences are blended by intermarriages; then the black and white is so far gone, that the species (for species they certainly are according to all common language) will keep to their type; in animals so far removed, with instinct in lieu of reason, there would probably be repugnance, and art required to make marriage. As Dr. Smith remarked, man and wild animals in this respect are differently circumstanced.

Is the shortness of life of *species* in certain orders connected with gaps in the *series of connections?* (If starting from same epoch *certainly.*) The absolute end of certain forms, from considering S. America (*independent of external causes*) does appear very probable: —

Mem. [i.e., Memento or Memorandum]: Horse, Llama, etc., etc.

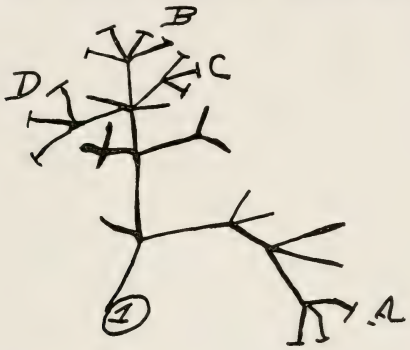
If we suppose (grant) similarity of animals in one country owing to springing from one branch, and the monucle[16] has definite life, then all die at one period which is not the case, *therefore monucle not definite life.*

I think: [Fig. 3.]

Thus between A and B immense gap of relation; C and B the finest gradation, B and D rather greater distinction. Thus genera would be formed, bearing relation to ancient types, with several extinct forms. For if each species (as ancient ①) is capable of making 13 recent forms,[17] twelve of the contemporarys [*sic*]

must have left no offspring at all,[18] so as to keep number of species constant.

With respect to extinction, we can easy see that variety of ostrich, Petise, may not be well adapted, and thus perish out, or on other hand like Orpheus being favourable, many might be produced. This requires principle that the permanent varieties produced by confined breeding and changing circumstances are continued and produced according to the adaptation of such



[Fig. 3]

Case must be that [in] one generation there should be as many living as now. To do this and to have [as] many species in same genus (as is) *requires* extinction.

circumstances, and therefore that death of species is a consequence (contrary to what would appear from America) of non-adaptation of circumstances. *Vide* two pages back — Diagram [Fig. 3].

The largeness of present genera renders it probable that many contemporary [species] would have left scarcely any types of their existence in the present world. Or we may suppose only each [i.e., certain] species in each generation only breeds; *like* individuals in a country not rapidly increasing.

If we thus go very far back to look to the source of the Mammalian type of organization, it is extremely improbable that any of the successors of his relations shall now exist. In same manner,

if we take (a man from) any large family of 12 brothers and sisters (in a state which does not increase) it will be chances against any one (of them) having progeny living ten thousand years hence; because at present day many are relatives, so that by tracing back the fathers would be reduced to small percentages. Therefore the chances are excessively great against any two of the 12 having progeny after that distant period.[19]

Hence if this is true, that the *greater the groups,* the *greater the gaps* (or *solutions of continuous structure*) *between them.* For instance, there would be great gap between birds and mammalia, still greater between Vertebrate and Articulata, still greater between animals and Plants. But yet, besides affinities from three elements, from the infinite variations, and all coming from one stock and obeying one law, they may approach; some birds may approach animals, and some of the vertebrates invertebrates. Just a few on each side will yet present some anomaly, and bearing stamp of some great main type, and the gradation will be sudden.

Heaven knows whether this agrees with Nature: *Cuidado.*[20]

The above speculations are applicable to non-progressive development, which certainly is the case at least during subsequent ages.

The Creator has made tribes of animals adopted [adapted?] preeminently for each element, but it seems law that such tribes, as far as compatible with such structures, are in minor degree adapted for other elements. Every part would probably be not complete, if birds were fitted solely for air and fishes for water. If my idea of origin of Quinarian System[21] is true, it will not occur in plants which are in far larger proportion terrestrial; if in any, in the Cryptogamic Flora (but not atmospheric types. Hence probably only four. Is not this Fries'[22] rule? What subject has Mr. Newman[23] the (7) man studied?)

The condition of every animal is partly due to direct adaptation and partly to hereditary taint; hence the resemblances and differences for instance of finches of Europe and America, etc., etc., etc.

The new system of Natural History will be to describe limits of form (and where possible the number of steps known). For

instance among the Carabidae. Instance in birds. Examine good collection of insects with this in view.

Geogr. Journal, Vol. VI, P. II, p. 89, Lieut. Wellsted[24] obtained many sheep from Arabian coast. "These were of two kinds, one white with a black face, and similar to those brought from Abyssinia, and the others dark brown, with long clotted hair resembling that of goats."

Progressive developement [*sic*] gives final cause for enormous periods anterior to man. Difficult for man to be unprejudiced about self, but considering power, extending range, reason and futurity it does as yet appear . . .[25]

In Mr. Gould's[26] Australian work some most curious cases of close but certainly distinct species between Australia and Van Diemen's Land,[27] and Australia and New Zealand. Mr. Gould says in subgenera they undoubtedly come from same countries. In mundine [*sic*] genera the nearest species often . . .[28]

. . . great S. American quadrupeds part of some great system acting over whole world; the period of the great quadrupeds declining as great reptiles must have once declined.

Cuvier[29] objects to propagation of species (read his Theory of the Earth attentively) by saying, why not have some intermediate forms been discovered between paleotherium, Megalonyx, Mastodon, and the species now living? Now according to my view, in S. America parent of all armadilloes might be brother to Megatherium; uncle now dead.

Bulletin Geologique, April 1837, p. 216, Deshayes[30] on change in shells from salt and F. water; on what is species. *Very Good.* (Has not Macculloch[31] written on same changes in fish?)

Mem.: Rabbit of Falklands described by I. and L.[32] as new species. Cuvier examined it . . .[33]

Same thing occurs with regards to other tribes in that same family.

(NB. I see Waterhouse thinks Quinary only three elements.)

How far does Waterhouse's[34] representatives agree with breeding in irregular trees and extinction of forms?? It is in simplest case saying every species in genus resembles each other (at least in one point, in truth in all excepting specific character); and in passing from species to genera, each retains some one character of all its family; but why so? I can see no reason

for these analogies; from the principle of atavism where real structures obliged to be altered, I can conceive colouring retained; therefore probably in some (heteromera) colouring of crysomela [*sic*][35] may be going back to common ancestor of Crysom. and Heterom., but I cannot understand the universality of such law.

It would be curious to know in plants (or animals) whether, in *races* have tendency to keep to either parent (this is what French call *atavism*). Probably this is first step in dislike to union; offspring not well intermediate.

Lyell,[36] Vol. III, p. 379.

Mammalian type of organization same from one period to another, preeminently Pachydermata, less so in Miocene and so on.

As I have traced the great Quadrupeds to Siberia, we must look to type of organization; extinct species of that country parents of American. Now Genera of these two countries ought to be similar.

Law?: existence *definite* without change, superinduced, or new species; therefore animals would perish if there were nothing in country to superinduce a change (?).

Seeing animal die out in S. America, with no change, agrees with belief that Siberian animals lived in cold countries and therefore not killed by cold countries. Seeing how horse and elephant reached S. America, explains how Zebras reached South Africa.

It is a wonderful fact, Horse, Elephant and Mastodon dying out about same time in such different quarters. Will Mr. Lyell say that some [same?] circumstance killed it over a tract from Spain to South America? *Never!* They die, without [i.e., unless] they change; like Golden Pippens [*sic*][37] it is a *generation* of *species* like generation of *individuals*. Why does individual die? To perpetuate certain peculiarities (therefore adaptation), to obliterate accidental varieties, and to accomodate [*sic*] itself to change (for of course change even in varieties is accomodation [*sic*]). Now this argument applies to species. If individual cannot procreate, he has no issue; *so with species.*

I should expect that Bears and Foxes, etc., same in N. America and Asia, but many species closely allied but different, because

country separated since time of extinct Quadrupeds. Same argument applies to England. Mem.: Shrew, Mice.

Animals common to South and North America. *Are there any?*

Rhinoceros peculiar to Java, and another to Sumatra. Mem.: Parrots peculiar, according to Swainson,[38] to certain islets in East Indian Archipelago. Dr. Smith considers probable true northern species replace the southern kinds.

(1) [*sic*] Gnu reaches Orange River and says so far will only go and no further.

Prof. Henslow says that when race once established so difficult to root out. For instance ever so many seeds of white flax, all would come up white, though planted in the same soil with blue. Now this is same bearing with Dr. Smith's fact of races of men.[39]

Strong odour of negroes, a point of real repugnance. Waterhouse says there is no TRUE *connection* between great groups.

Speculate on land being grouped towards centre near Equator in former periods, and then splitting off.

If *species* generate other *species* their race is not utterly cut off; like golden pippen [*sic*], if produced by seed go on, otherwise all die. The fossil horse generated in S. Africa Zebra, and continued, perished in America.

All animals of same species are bound together just like buds of plants, which die at one time, though produced either sooner or later.

Prove animals like plants, trace gradation between associated and nonassociated animals, and the story will be complete.

It is absurd to talk of one animal being higher than another. *We* consider those, when the intellectual faculties (cerebral structure) most developed, as highest. A bee doubtless would when the instincts were . . .[40]

. . . there appears in Australia great abundance of species of few genera or families (long separated).

Proteaceae and other forms (?), being common to Southern hemisphere, does not look as if S. Africa peopled from N. Africa.

An originality is given (and power of adaptation is given by *true* generation) through means of every step of progressive increase of organization being imitated in the womb (which has been passed through to form that species). (Man is derived from Monad each fresh —)[41]

Mr. Don[42] remarked to me, that he thought species became obscurer as knowledge increased, but genera stronger. Mr. Waterhouse says no real passage between good genera. How remarkable spines, like on a porcupine, on Echidna.

Good to study Regne Animal for *Geography*.[43]

The motion of the earth must be excessive up and down: Elephants in Ceylon, East India Archipelago; West Indies. Opossum and Agouti same as on continent (3 Paradiseini are common to Van Diemen's Land and Australia). From the consideration of these archipelago's ups and downs [they are] in full conformity with European formations (England and Europe, Ireland, common animals); for instance tertiary deposits between East India islets.

Ireland longer separated; hare of two countries different. Ireland and Isle of Man possessed elk, not England. Did Ireland possess Mastodons?? (Negative facts tell for little.)

Geographic distribution of Mammalia more valuable than any other, because less easily transported. Mem.: plants on Coral islets. Next to animals, land birds, and life shorter or change greater.

In the East Indian Archipelago it would be interesting to trace limits of large animals.

Owls transport mice alive?

Species formed by subsidence: Java and Sumatra Rhinoceros; elevate and join, keep distinct, two species made. Elevation and subsidence continually forming species. (Man and wife being constant together for life is in accordance with . . .)

(The male animal affecting *all* the progeny of female insures of the mixing of individuals.)

South Africa, proof of subsidence and recent elevation: pray ask Dr. Smith to state that most clearly.

Fox tells me that beyond all doubt seeds of Ribston Pippin produce Ribston Pippin, and Golden Pippin, goldens, hence *subvarieties,* and hence possibility of reproducing any variety, although many of the seeds will go back. Get instances of a *variety* of fruit tree or plant run wild in foreign country. (Here we have avitism [*sic,* i.e., atavism] the ordinary event and succession the extraordinary.)

When one sees nipple on man's breast, one does not say some use, but sex not having been determined, so with useless wings under elytra of beetles, born from beetles with wings, and modified. If simple creation surely would have been born without them.

In some of the lower orders a perfect gradation can be found from forms marking good genera by steps so insensible that each is not more change than we know *varieties* can produce. Therefore all genera *may* have had intermediate steps. Quote in *detail* some good instance.

But it is other question, whether there have existed *all* those intermediate steps especially in those classes where species not numerous. (N.B., in those classes with few species greatest jumps strongest marked genera? Reptiles?) For instance there never may have been grade between pig and tapir, yet from some common progenitor. Now if the intermediate ranks had produced infinite species, probably the series would have been more perfect, because in each there is possibility of such organization (spines in Echidna and Hedgehog). As we have one marsupial animal in Stonefield [*sic*][44] slate, the father of all Mammalia in ages long past, and still more so known with fishes and reptiles. In mere eocine [*sic*] rocks we can only expect some steps. I may ask whether the series is not more perfect by the discovery of fossil Mammalia than before, and that is all that can be expected. This answers Cuvier.

Perhaps the father of Mammalia as Heterodox as ornithorhyncus [*sic*]. If this last animal bred, might not new classes be brought into play?

The father being climatized, climatizes the child. Whether every animal produces in course of ages ten thousand varieties (influenced itself perhaps by circumstances) and those alone preseved which are well adapted? This would account for each tribe acting as in vacuum to each other.

p. 306. Chamisso on Kamtschatka quadrupeds; Kotzebue first voyage.[45] Entomological Magazine, paper on Geographical range. Richardson,[46] Fauna Borealis.

It is important the possibility of some island not having large quadrupeds. Humboldt[47] has written on the geography of plants. Essai sur la Geographie des Plants, I Vol. in 4° —

I have abstracted Mr. Swainson's[48] trash at beginning of volume on Geographical distribution of animals.

Geograph. Journal,[49] Vol. I, p. 17-21, says from Swan river along South coast all the remarkable Australian genera collected together.

Man has no *hereditary prejudices* or instinct to conquer, or breed together. Man has no limits to desires; in proportion instinct more, reason less, so will aversion be.

L'Institut,[50] (1837, no. 246) a section of fossil "singe,"[51] it cannot be made to approach the Colobes [*sic*][52] which in South Africa appears to represent the semnopitheque[53] of India. Tooth of Sapajou.[54] Sapajou is S. American form. Therefore it is like case of great edentate (has been doubted) and opossum found in Europe now confined to southern hemisphere. (If these facts were established it would go to show a *centrum* for Mammalia.) I really think a very strong case might be made out of world before Zoological divisions. Mem.: Species doubtful when known only by bones. Mem.: Silurian fossils. How are South American shells?

Do not plants which have male and female organs together, yet receive influence from other plants? Does not Lyell[55] give some argument about varieties being difficult to keep on account of pollen from other plants?; because this may be applied to [all], show all plants do receive intermixtures. But how with hermaphrodite shells!!!?

We have not the slightest right to say there never was common progenitor to mammalia and fish, when there now exists such strange forms as ornithorhyncus [*sic*].

The type of organization constant in the shells.

The question if creative power acted at Galapagos it so acted that birds with plumage and tone of voice purely American, North and South; so permanent a breath cannot reside in space before island existed. Such an influence must exist in such spots. We know birds do arrive, and seeds. (And geographical divisions are arbitrary and not permanent. This might be made very strong, if we believe the Creator created by any laws, which I think is shown by the very facts of the Zoological character of these islands.)

The same remarks applicable to fossil animals same type; armadillo-like cray [i.e., crayfish?] created; passage for vertebrae in neck same cause. Such beautiful adaptations, yet other animals live so well. This view of propagation gives a hiding place for many unintelligible structures; it might have been of use in progenitor, or it may be of use, — like mammae on man's breast.

How does it come wandering birds such [as] sandpipers not new at Galapagos? Did the creative force know that these species could arrive? Did it only create those kinds not so likely to wander? Did it create two species closely allied to Mus. coronata,[56] but not coronata? We know that domestic animals vary in countries without any assignable reason.

Astronomers might formerly have said that God ordered each planet to move in its particular destiny. In same manner God orders each animal created with certain form in certain country, but how much more simple and sublime power: let attraction act according to certain law; such are inevitable consequences. Let animals be created, then by the fixed laws of generation, such will be their successors.

Let the powers of transportal be such, and so will be the forms of one country to another. Let geological changes go at such a rate, so will be the number and distribution of the species!! It may be argued representative species chiefly found where [there are] barriers (and what are barriers by?), interruption of communication, or when country changes. Will it [be] said that volcanic soil of Galapagos under equator, that external conditions, would produce species so close as Patagonian Cha — [57] and Galapagos Orpheus? Put this strong, so many thousand miles distant.

Absolute knowledge that species die and others replace them. Two hypotheses: [1] fresh creations is mere assumption, it explains nothing further; [2] points gained if any facts are connected.[58] No doubt in birds, mundine [*sic*] genera (Bats, Foxes, Mus) are birds that are apt to wander and of easy transportal. Waders and waterfowl. Scrutinize genera, and draw up tables. Instinct may confine certain birds which have wide powers of flight; but are there any genera mundine which cannot transport easily (it would have been wonderful if the two Rheas had existed in different continents)? In plants I believe not.

It is a very great puzzle why Marsupials and Edentata should only have left off springs [*sic*] in or near South Hemisphere. Were they produced in several places and died off in some? Why did not fossil horse breed in S. America? It will not do to say period unfavourable to *large* quadrupeds; horse not large.[59]

. . . but not vice versa. (Could plants live without carbonic acid gas?) Yet unquestionably animals most dependent on vegetables, of the two great Kingdoms.

Principes de Zool. Philosop.:[60] I deduce from extreme difficulty of hypothesis of connecting mollusca and vertebrata, that there must be very great gaps, yet some analogy. The existence of plants, and their passage to animals appears greatest argument against theory of analogies.

States there is but one animal: one set of organs; the other animals *created* with endless differences; does not say propagated, but must have concluded so. Evidently considers (or hints) generation as a short process, by which one animal passes from worm to man (highest) as typical of changes which can be traced in *same* organ in *different* animals in scale. In monsters also *organs* of lower animals appear, yet nothing about propagation. I see nothing like grandfather of Mammalia and birds, etc. P. 32,[61] reference to M. Edwards' law of crustacea, with respect to mouth, those beautiful passages from one to other organ; Cuvier on opposite side: V. [i.e., *Vide*] Vol. of Fish, p. 59,[62] Cuvier has said each animal made for itself does not agree with old and modern types being constant. Cuvier's theory of *Conditions* of existence is thought to account [for] resemblances, etc., therefore Quinary system, or three elements (p. 68).

With unknown limits, every tribe appears fitted for as many situations as possible (*conditions will not explain states*) *for instance take birds, animals, reptiles, fish.* (*Perhaps consideration of range of capabilities past and present might tell something.*)

P. III., G. St. Hilaire.[63]

Insects and Molluscs allowed to be wide hiatus; states in one the sanguineous system, in other nervous developed; (Owen's idea); states these class[es] approach on the confines? Balanidae? I cannot understand whether G. H. [Geoffroy St. Hilaire] thinks development in quite straight lines, or branching.

G. H.: What does the expression mean, used by Cuvier, that all animals (though some maybe) have not been created on the same plan? (Second resumé well worth studying.) H. says grand idea God giving laws, and then leaving all to follow consequences. I cannot make out his ideas about propagation. *His work: Philosophie Anatomique*[64] (*2nd Vol. about monsters worth reading*).

N.B. Well to insist upon (different animals)[65] large Mammalia not being found on all islands (if act of fresh creation why not produced on New Zealand?); if generated an answer can be given.

It is a point of great interest to prove animals not adapted to each country. Provision for transportal (otherwise) not so numerous; quote from Lyell. Assuming truth of quadrupeds being created on small spots of land, of the same type with the great continents, we get a means of knowing of movements.

How can we understand excepting by propagation that out of the thousands of new insects all belong to same types already established? Why out of the thousand forms should they all be classified [i.e., classifiable]? Propagation explains this.

Ancient Flora thought to [be] more uniform than existing. Ed. N. Philosp. Jr.,[66] p. 191, no. 5, Apr. 1827.

F. Cuvier[67] says, "But we could only produce domestic individuals and not races, without the occurrence [i.e., concurrence][68] of one of the most general laws of life, the transmission of [the organic or intellectual modifications by generation. Here one of the most astonishing phenomena of nature manifests itself to us, the transformation of][69] a fortuitous modification into a durable form, of a fugitive want into a fundamental propensity, of an accidental habit into an instinct." Ed. N. Phi. J. p. 297, No. 8, Jan.-Apr. 1828. I take higher grounds and say life is short for this object and others, viz., not too much change.

In Number 6 of Ed. N. Philo. Journ., Paper by Crawford[70] on Mission to Ava, account of *hairy* man (because ancestors hairy), with one hairy child, and of *albino* (*disease*) being banished and given to Portuguese priest. In first settling a country, people very apt to be split up into many isolated races! Are there any instances of peculiar people banished by rest? (Therefore most monstrous forms have tendency to propagate, as well as diseases.)

In intermarriages, smallest differences blended; rather stronger tendency to imitate one of the parents; repugnance generally to marriage before domestication; afterwards none or little, with fertile offspring; marriage never probably excepting from strict domestication, offspring not fertile, or at least most rarely and perhaps never female. No offspring: physical impossibility of marriage.

Whether those genera which unite very different structure, as *petrel* and *alk* [*sic*], do [they] not show the possibility of common branching off?

Accra.[71] Coast of Africa. Clay slate. Strike SSW and NNE, dip 30°-80° (?). Ed. Phil. N. J. p. 410, 1828.

It is daily happening that Naturalist[s] describe animals as species, for instance Australian dog, or Falkland rabbit. There is [i.e., are] only two ways of proving to them it is not; one, when they can [be] proved descendant, which of course most rare, or when placed together they will breed. But what a character is this?[72]

The relation of Analogy of Macleay,[73] etc., appears to me the same, as the irregularities in the degradation of structure of Lamarck, which he says depends on external influences. For instance he says wings of bat are from external influence. Hence name of analogy, the structures in the two animals bearing relation to a third body,[74] or common end of structure.

A Race of domestic animals made from influences in one country is permanent in another. (Good argument for species not being so closely adapted.)

Near the Caspian (Province of Ghilan) wooded district cattle with humps as in India. Geograph. J.,[75] Vol. III, P. I, p. 17. (Lat. 37° about.)

Vol. IV, P. I, Geograp. Journal, Voyage up the Massaroony, by W. Hillhouse [*sic*].[76] Demerara. In note, Demerara, 10 (12) feet beneath surface, forest trees fallen (kind well known, carbonized), clay fifty feet, then forest 120 feet, micaceous rocks: subsidence appears indicated, p. 36.

Geograp. Journ. Vol. IV, P. II, p. 160,[77] Melville Island. "The buffaloes, introduced from Timor, herded separate from the English cattle, nor could we get them to associate together."

There is long rigmarole article by G. Hilaire[78] on wonder of finding monkey in France, of genus peculiar to East Indian islands. Compares it to fossil Didelphus (S. American genus) in plaster of Paris. Now this is exception to *law of type,* like horse in S. America, or like living Edentata in Africa, etc., etc. Now if suppose world more perfectly continental, we might have wanderers (as Peccari in N. America); then if it is doomed that only one species of family has offspring, the *chance* is that these wanderers would not, but where original forms most numerous, then would be wanderers. Some however might have offspring, and then we should have anomalies, as Cape Anteater (V. [i.e., *Vide*] L'Institut,[79] p. 245, 1837). This supposes world divided into Zoological provinces — united — and now divided again. Weakest part of theory death of species without apparent physical cause. Mem.: Mastodon all over S. America. Hilaire does not seem (?) to consider the monkey as a wanderer, but as produced by climate?

M. Baer[80] (thinks) the Auroch was found in Germany and thinks even now in central and Eastern Asia beyond the Ganges and perhaps even in India, p. 261, L'Institut, 1837.

Mem.: Sir F. Darwin,[81] cross-breed boars were wilder than parents, which is same as Indian Cattle, therefore tameness not hereditary? Having been gained in short time.

Milvulus forficatus[82] has a wide range, is a Tyrant flycatcher doing the service of a swallow.

I think we may conclude from Australia and S. America that only some mundine cause has destroyed animals over the whole world. For instance gradual reduction of temperature from geographical or central heat. But then shells — .

Mr. Yarrell[83] says that old *races* when mingled with newer, hybrid variety partakes chiefly of the former.

Eyton's[84] paper on Hybrids, Loudon's Magazine.

Gould[85] on Motacilla, Loudon Mag., September or October, 1837. Species peculiar to Continent and England.

Westwood[86] has written paper on affinity and analogy in Linnaean Transactions.

Mr. Wynne[87] distinctly says that the mixture between Chinese and English Breed decidedly exceedingly prolific, and hybrid

about half-way. Eyton says hybrid about half aways [*sic*] and result the same.

Indian cattle and common produced very fine hybrid offspring, much larger than the dam, from those imported by Dr. (Ld.) Powis.[88]

Hybrid dog's offspring seldom intermediate between parents. How easily does wolf and dog cross? Mr. Yarrel [*sic*] thinks oldest variety impresses the offspring most forcibly, Esquimaux dog and Pointer. (Game fowls have courage independently of individual force.)

Mr. Wynne has crossed Ducks and Widgeon and offspring, either amongst themselves, or with parent birds. (W. Fox[89] knew of case of male widgeon, winged, and turned on pool, first season bred readily with common ducks.)

Kirby[90] all through Bridgewater errs greatly in thinking every animal born to consume this or that thing. There is some much higher generalization in view.

In marsupial division do we not see a splitting in orders, carnivora, rodents, etc., JUST COMMENCING!!?

Kirby says (not definite information) west of Rocky Mountains Asiatic types discoverable.

Bridgewater Treatise, p. 85 [Vol. I]. Parasite of Negroes different from European. Horse and ox have different parasite in different climates.

Humb. (Humboldt?)[91] Vol. V, P. II, p. 565. Consult. Says types most subject to vary where intermixtures precluded.

There are some good accounts of passages of legs into mouth-pieces of Crustacea. (Kirby, Bridgewater Treatise.) Vol. II, p. 75. A Fish which emigrates over land is a silurus, p. 123. A climbing fish, p. 122.

A Terrestrial annelidous animal, p. 347. Vol. I[92] compare with my planaria; leaches out of water.

Does the odd Petrel of T. del F. [Tierra del Fuego] take form of auk because there is no auk in Southern Hemisphere? Does this rule apply?

A Treatise on Form of animals by Mr. Cline.[93] "The character of both parents are observed in their offspring, but that of the male more frequently predominates." p. 20, ditto. "If hornless ram be put to horned ewe almost all the lambs will be hornless."

(Does this apply to where same animal breeds often with same female?) p. 28, "It is wrong to enlarge a native breed of animals, for in proportion to their increase of size they become worse in form, less hardy, and more liable to disease."

If population of place be constant (say 2000) and at present day every ten living souls on average are related to the 200th year degree, then 200 years ago there were 200 people living who now have successors. Then the chance of 200 people being related within 200 years backward might be calculated and this number eliminated. Say 150 people four hundred years since were progenitors of present people, and so on backwards to one progenitor, who might have continued breeding from eternity backwards.

If population was increasing between each lustrum, the number related at the first start must be greater, and this number would vary at each lustrum, and the calculation of chance of the relationship of the progenitors would have different formula for each lustrum. [A lustrum is a five year census.]

We may conclude that there will be a period, though long distant, when of the present men (of all races) not more than a few will have successors. At present day in looking at two fine families one will [have] successors for centuries, the other will become extinct. Who can analyze causes: dislike to marriage (some delay), disease, effects of contagions and accidents. Yet some causes are evident, as for instance one man killing another. So is it with *varying* races of man; then races may be overlooked: many variations consequent on climate, etc.; the whole races act towards each other, and are acted on, just like the two fine families (no doubt a different set of causes must act in the two cases).

May this not be extended to all animals? First consider species of cats, other tribes, etc., etc. (Exclude mothers and then try this as simile.)

In a decreasing population at any one moment fewer closely related; therefore (few species of genera) ultimately few genera (for otherwise the relationship would converge sooner), and lastly, perhaps some one single one. Will not this account for the odd genera with few species which stand between great groups, which we are bound to consider the increasing ones?

N.B. as illustrations, are there many anomalous lizards living, or of the tribe fish extinct, or of Pachydermata, or of coniferous trees, or in certain shell cephalopoda? Read Buckland.[94]

L'Institut, 1837, p. 319, Brongniart,[95] no dicotyledonous plants and few monocot. in coal formation (?). P. 320, states Cryptogam. Flora formerly common to New Holland?! P. 320, says Coniferous structures intermediate between vascular or Cryptogam. (original Flora) and Dicotyldones, which nearly first appear (p. 321) at Tertiary epochs. P. 330, Fossil Infusoria found of unknown forms, a circumstance undiscovered by Ehrenbergh [*sic*].[96]

Indian cow with hump and common; between Esquimaux and European dog? Yet man has had no interest in perpetuating these particular varieties.

If species made by isolation, then their distribution (after physical changes) would be in rays from certain spots. (Agrees with old Linnaean doctrine and Lyell's to certain extent.)

Von Buch, Canary Islands, French Edit.:[97] Flora of Islands very poor (p. 145) 25 plants; 36 St. Helena, without ferns, analogous to nearest continent; poorness in exact proportion to distance (?) and similarity of type (?) (Mem.: Juan Fernandez). From study of Flora of islands, "ou bien encore on pourrait au plus en conclure quels sont les genres qui, sous ce climat, se divisent le plus aisément en espèces distinctes et permanentes." p. 145. In Humboldt[98] great work de distribut., Plantarum, relation of genera to species in France is 1:5, 7; in Laponia 1:2, 3.

(Mem.: Lyell[99] on shells.)		genera
In:	North Africa	1:4,2
	Iles Canaries	1:1,46
	St. Helena	1:1,15

Calculate my Keeling case; Juan Fernandez, Galapagos, Radack Isle? Therefore islands and arctic are in same relation. We find species few in proportion to difficulty of transport. For instance the temperate parts of Teneriffe, the proportion of genera 1:1. I can understand in one small island species would not be manufactured. Does it not present analogy to what takes place from time? Von Buch distinctly states that permanent varieties become species, p. 147, p. 150, not being crossed with others.

Compares it to languages. But how do plants cross? — admirable discussion.[100]

Mr. Owen[101] suggested to me, that the production of monsters (which Hunter[102] says owe their origin to very early stage) and which follow certain laws according to species, present an analogy to production of species.

Animals have no notions of beauty, therefore instinctive feelings against other species (for sexual ends), whereas man has such instincts very little.

In Zoology Proceedings, Jan. 1837 by Eyton,[103] account of three kinds of pigs; difference in skeletons; *very good.*

Apteryx, a good instance probably of rudimentary bones. As Waterhouse[104] remarked, mere length of bill does not indicate affinity because similar habits produce similar structures. Mem.: Ornitho Rhyncus [*sic*]. Would not *relationship* express a real affinity, and affinity, [e.g.?] whales and fish?

Progeny of Manks cats without tails; some long and some short; therefore like dogs. Ogleby [*sic*][105] says Wolves at Hudson Bay breed with dogs, the bitches never being killed by them, whilst they eat up the dogs.

L'Institut. Curious paper by M. Serres[106] on Molluscous animals representing foetuses of vertebrata, etc., 1837, p. 370. Owen says nonsense.

The distribut[ion] of big animals in East Indian Archipelago, very good in connection with Von Buch Volcanic chart and my idea of double line of intersection. At India House collection of Birds from Java, at Leyden series from several islands. Bear peculiar to Sumatra and not found on Java. Monkey peculiar to latter, not to former. (Dr. Horsfield.)[107]

Consult Dr. Smith History of S. African Cattle;[108] Phillips[109] Geology, p. 81 in Lardner's Encyclop., proportion between fossils and recent shells, between herbivorous and zoophagous mollusca according to periods. N.B., was Europe desert (like S. Africa) after Coal Period?

In those divisions of molluscs where species now least in number (as Cephalopods) in last tertiary epochs, [were] most genera dead? Examine into this (in Phillips). According to this, formerly there would have been many genera of monobranchous animals, p. 82. (There are many tables in Phillip's of numerous

genera in fossil and recent state well worth consideration.) Tabulate Mammalia on this principle.

Man (Varieties-Races) in *savage* state may be called species (races); in *domesticated* [state] species (races). If all men were dead, then monkeys make men. Men make angels.

Those species which have long remained are those (?Lyell?) which have wide range and therefore cross and keep similar. But this is difficulty: this immutability of some species. [Fig. 4.]

[Fig. 4]

In Phillips p. 90, it seems the most organized fishes lived far back. Fish approaching to reptiles at Silurian age.

How long back have insects been known? As Gould remarked to me, the "beauty of species is their exactness," but do not known varieties do the same? May you not breed ten thousand greyhounds and will they not be greyhounds?

Yarrell's remark about old varieties affecting the cross most well worthy of observation.

I think it is certain, strata could not now accumulate without [including] sealbones and cetaceans, both found in every sea, from Equatorial to extreme poles. Oh, Wealden, — Wealden.[110]

Do the N. American Tertiary deposits present analogies to shells of living seas?[111]

A breed of Blood Hounds from Aston Hall close to Birmingham, and supposed to be descended from a breed known to be there since the time of Charles, and now in the possession of Mr. Howard Galton,[112] have one of the vertebra, about ⅔ from base of tail, enlarged two [*sic*] very considerably, so that any person would say the tail was broken. This came so often that it was difficult to obtain a litter without this defect. Very curious case — W. D. Fox.

When dogs are bred into each other the females loose [*sic*] desire, and it is required to give the cantharinides.[113]

Bull. Soc. Geolog., 1834, p. 217 Java. Fossils 10 out of twenty have *analogues* (uses this word for similar) in the Indian sea. Deshayes.[114]

Mr. McClay [115] is inclined to think that offspring of Negro and white will return to native stock (the cross often whiter than white parent). The mulattos [*sic*] themselves explain it by intermarriages with people either a little nearer black or white as it may happen. Dr. Smith [116] says he is sure of the case at Cape. McClay argues from it Black and White species. For says he seeds of hybrid lillies, etc., etc., etc., (V. Herbert [117] on hybrids) thus act. Now the point will be to find whether known varieties in plants do so, as in cacti, etc., etc.; as in dogs; investigate case of pidgeons [*sic*], fowls, rabbits, cats, etc., etc. When black and white men cross some offspring black, others white, which is more closely allied to case of cross of dogs. See paper in Philosoph. Transactions on a quagga and mare crossing, by Ld. Moreton [*sic*] [118] where mare was influenced in this cross to after births, like aphides. Case of boy with foetus developed in breast looks as if many ova impregnated at once. Dr. Smith considers the Caffers [i.e., Kaffirs] (like Englishmen), men of many countenances, as hybrid race. Is not this contradiction to his view of races not mingling?

In Foxes [*sic*] case of Blood Hounds, a little mingling would probably have been good, namely such as blood hounds from other parts of England. Mr. Bell of Oxford St. had a very fine bloodhound bitch which would never take the dog. But at last a rough-haired shepherd dog lined [i.e., bred] her and produced a very large litter; never afterwards went in heat. This is good instance of same fact in Mr. Galton's case. It explains the loss (and expense) (must probably have occurred to everyone) of rare breeds of dogs from owners great care of them. Fox says when two dogs of opposite breeds are crossed, sometimes offspring quite intermediate, sometimes take strongly after either parent, about as often one way as other. He has known case of good pointer and rough water spaniel produce litter like both parents and Mr. Bell has half bloodhound and grey hound.

Where two dogs have lined bitch directly one after the other, puppies differ and like both parents. Fox told me of case of mare covered by blood horse and carthorse, two folds [*sic*].[119]

Mr. Herbert's [120] papers are in the Horticultural Transactions and a distinct work on hybridity under title of Amaryllidae and Narcissus. (Mr. Donn [121] considers Mr. H. rather wild.)

Mr. Donn remarked to me that give him a species from Ireland, England, Scotland, and other localities and each one will have a peculiar constant aspect. That is, varieties though of trifling order are formed by nature.

Carmichael,[122] Tristan D'Acunha, a list of its Flora is given. Mr. Don [*sic*] remarked to me that some good African and some good S. American forms (and daresays some of these forms would have some [same?] peculiarity). Now when we hear that the whole island is volcanic surmounted by crater and studded with others, we see a beginning to island. Graham Island. We know many seeds might be transported, some blown, — floating trees. Thrushes (Turdus Guyanensis?), and bunting (Emberiza Brasiliensis?), and coots (Fulica chloropus) might bring in stomach, etc., etc. (Mem.: discover what kinds of seeds, then plants.) Mem.: Fact stated by Mr. Don in island Teneriffe, St. Helena, J. Fernandez, Galapagos. Many trees compositae (Ferns ditto), because seeds first arrived and hence formed trees, and would creator (on volcanic island) *make* plants (grow closely) when this volcanic point appeared in the great ocean, have made plants of American and African form merely because intermediate position? We cannot consider it as adaptation because volcanic island, whilst Africa [is] sandstone and granite (that is genera near Cape); see if there are any species same as T. del Fuego and C. of Good Hope; show *possibility* of transport. If some cannot be explained, more philosophical to state we do not know how transported. Glaciers might have acted at Tristan D'Acunha. Carmichael, Linn. Transact., Vol. XII.

The Alpine plants of the Alps must be new formations because snow formerly descended lower, therefore species of lower genera altered, or northern plants. No. Mem.: The Antarctic flora must formerly have been separated by short space from mountains low down, therefore plants common. Take an example from T. del. Fuego.

Ellis (?)[123] says Tahitian kings would hardly produce from Incestuous intercourse, a parallel fact to Blood Hounds.

Before attract. of gravity discovered, it might have been said it was as great a difficulty to account for movement of all [planets],[124] by one law, as to account for each separate one, so to say that all Mammalia were born from one stock, and since distributed

by such means as we can recognize, may be thought to explain nothing, it being as easy to produce (for the creator) two quadrupeds (Jaguar and Tiger) at S. America.[125]

When species cross and hybrids breed, their offspring show tendency to return to one parent, this is only character, and yet we find this same tendency (only less strongly marked) between what are called varieties. N.B., one mother bringing forth young having very different characters is attempt at returning to parent stock. I think we may look at it so, — ?? It holds good even with trifling differences of expression, one child like father, another like mother.

Has Lowe[126] written any other paper besides one in Latin, one on Madeira? Any general observations? Difference of species between land shells of Porto Santo and Madeira. I believe very curious.

My idea of propagation almost infers what we call improvement. All Mammalia from one stock, and now that one stock cannot be supposed to be most perfect (according to our ideas of perfection), but intermediate in character. The same reasoning will allow of decrease in character (which perhaps is case with fish, as some of the most perfect kinds, the shark, lived in remotest epochs). Lizards of secondary period in same predicament? It is another question, whether whole scale of Zoology may not be perfecting by change of Mammalia for Reptiles, which can only be adaptation to changing world. I cannot for a moment doubt but what cetaceae and Phocae now replace Saurians of Secondary epoch; it is impossible to suppose such an accumulation at present day and not include Mammalian remains. The Father of all insects gives same argument as father of Mammals, but have improvement in system of articulation. Whether type of each order may not be supposed that form which has wandered least *from* ancestral form? If so are present typical species most near in form to ancient? In shells alone can this comparison be instituted.

People often talk of the wonderful event of intellectual man appearing. The appearance of insects with other senses is more wonderful; its mind more different probably, and introduction of man nothing compared to the first thinking being, although hard to draw line; not so great as between perfect insect, etc.

Forms hard to tell, whether articulata, or intestinal, or even mite. A bee (compared with cheese mite) with its wonderful instincts (might well say how —). The difference is that there is a wide gap between man and next animals in mind, more than in structures.

If the skeleton of a negro had been found, what would Anatomists have said? Where is Pentland's[127] account of . . . ?[128]

A, B, C, D. (A) crossing with (B), and (B) being crossed with (C) prevents offspring of A becoming a good species well adapted to locality, but it is instead a stunted and diseased form of plant, adapted to A, B, C, D. Destroy plants B, C, D, and A will soon form good species!

The increased fertility of slightly different species and intermediate character of offsprings accounts for *uniformity* of species. We must confess that we cannot tell what is the amount of difference which improves and checks it. It does not bear any precise relation to structure. (Mem.: Eyton's[129] Hogs and Dogs.)

The passage in last page explains that between species from moderately distant countries there is no test but generation (but experience according to each group) whether good species, and hence the importance naturalists attach to Geographical range of species.

Definition of species: one that remains at large with constant characters, together with other beings of very near structure. Hence species may be good ones and differ scarcely in any external character; for instance two wrens forced to haunt two islands, one with one kind of herbage, and one with other, might change organization of stomach and hence remain distinct. Where country changes rapidly we should expect most species.

The difference [in] intellect of man and animals not so great as between living things without thought (plants), and living things with thoughts (animals). (Therefore my theory very distinct from Lamarck's.) Without *two* species will generate common kind, which is not probable;[130] then monkeys will never produce man, but both monkeys and man may produce other species. Man already has produced marked varieties and may someday produce something else, but not probable owing to mixture of races. When all mixed and physical changes (intellectual[ity]

being acquired alters case?), other species or angels produced.

Has the Creator since the Cambrian formation gone on creating animals with same general structure? Miserable, limited view. With respect to how species are, Lamarck's "willing" doctrine absurd. As equally are arguments against it, namely how did otter live before being modern otter? Why to be sure there were a thousand intermediate forms. Opponent will say, show them me. I will answer yes, if you will show me every step between bull Dog and Greyhound. I should say the changes were effects of external causes, of which we are as ignorant as why millet seed turns a Bullfinch black (or iodine on glands of throat), or colour of plumage altered during passage of birds (where is this statement, I remember L. Jenyns talking of it?), or how to make Indian cow with hump and pig's foot with cloven hoof.

Ask Entomologists whether they know of any case of *introduced* plant, which an insect has become attached to, that insect not being called omniphitophagous [*sic*]. But it will be said there are latent insects, as crows against man with gun, and Bustards, etc., etc.!!!

An American and African form of plant being found in Tristan D'Acunha may be said to deceive man as likely as fossils in old rocks for same purpose!!

Can the wishing of the Parent produce any character on offspring? Does the mind produce any change in offspring? If so [is] adaptation of species *by generation* explained? N.B. Look over Bell [131] on Quadrupeds for some facts about dogs, etc., etc. N.B. Animals very remote, ass and horse produce offspring exactly intermediate. Reference to pig and dogs.

My theory will make me deny the creation of any new quadruped since days of Didelphus in Stonefield [*sic*] [132] therefore all lands united (Falkland Fox, ice). Mauritius, what a difficulty, where elevation, subsidence near is only hope. New Zealand (compare to Van Dieman's land), glorious fact *of absence of quadrupeds*. East India Archipelago very good on opposite tendency.

Study Ellis and Williams,[133] Zoology of South Sea islands. Any animals? I believe none. Canary islands? Madeira? Tristan D'Acunha? Iceland? The connection between Mauritius and Madagascar very good; Fernando Po and Coast of Africa equally

good. Small island off New Guinea same fact. See Coquille's Voyage.[134] Galapagos mouse (brought by canoes) (?). Ceylon and India; Van Diemen's land; Australia; England and Europe. It will be well worth while to study profoundly the origin and history of every terrestrial Mammalia, especially moderately large ones.

Is the Flora of Tierra del Fuego like that of North Europe, many genera and few species?

The number of genera on islands and on Arctic shores evidently due to the chance of some ones of the different orders being able to survive or chance having transported them to new station. When the new island splits and grows larger, species are former [i.e., formed] of those genera (and hence by same chance few representative species). (This must happen, and then enquiry will explain representative Systems.) Of this we see example in English and Irish Hare, Galapagos' shrews, and when big continent, many species belonging to its own genera. Therefore if in small tract we have many species, we may insure mass continental or many large islands. Hence this must have been condition of Paris basin land. (How is this with Fernando Po, with plants of St. Helena and Tristan D'Acunha?) If on one island several species of same genus, subsided land, Mauritius? (Resolves itself into question of proportion of species to genus.) Although the Horse has perished from S. America, the jaguar has been left, and fox, and bear. If I had not discovered channel of communication by which great Edentata might have roamed to Europe and Pachydermata from Europe to America, how strang [*sic*] would presence of Jaguar [have] been in S. America?

W. Coast of Africa and E. of America ought to present great contrast in forms. India intermediate, see how that is.

Are shell-boring [shell-bearing] molluscs like Carnivorous Mammalia in their wide range and in their duration of species? (Are carnivorous Mamm. in Paris basin allied to present, [i.e.,] more like present Carnivora than Pachydermata?)

If my theory true, we get: (1st.) a *horizontal* history of earth within recent times and many curious points of speculation; for having ascertained means of transport, we should then know whether former lands intervened; (2nd.) by character of any two ancient fauna, we may form some idea of connection of those

two countries (hence India, Mexico, and Europe, one great sea; coral reefs; therefore shallow water at mtns. [form] the islands); (3rd.) we know that structure of every organ in A.B.C., three species of one genus, can pass into each other (by steps we see); but this cannot be predicated if structures in two genera. (We then cease to know the steps.) [135] Although D.E.F. follow close to A.B.C., we cannot be sure that structure (C) could pass into (D). We may foretell species, limits of good species being known. It explains the blending of two genera. It explains typical structure. Every species is due to adaptation and hereditary structure (*latter far* chief element, therefore little service habits in classification, or rather the fact that they are *not* [by] far the most serviceable). We may speculate of durability of succession from what we have seen in old world and on amount [of] changes which may happen. *It leads you to believe the world older than* GEOLOGISTS *think. It agrees with excessive inequality of numbers of species in divisions. Look at articulata!!!* It leads to nature of physical change between one group of animals and a successive one. It leads to knowledge what kinds of structure may pass into each other; now on this view no one need look for intermediate structure, say in brain between lowest Mammal and Reptile (or between extremities of any great divisions). Thus a knowledge of possible changes is discovered for speculating on future. Therefore fish never become a man. Does not require fresh creation. If continent had sprung up round Galapagos on Pacific side, the Oolite [136] order of things might have easily been formed. With belief of transmutation and geographical grouping we are led to endeavour to discover *causes* of change, the manner of adaptation (wish of parents??); instinct and structure become full of speculation and line of observation. View of generation being condensation, test of highest organization intelligible; may look to first germ, led to comprehend two affinities. My theory would give zest to recent and fossil Comparative Anatomy, it would lead to study of instincts, heredity and mind heredity, whole metaphysics. It would lead to closest examination of hybridity and generation, causes of change in order to know what we have come from and to what we tend, to what circumstances favour crossing and what prevents it; this, and direct examination of direct passages of structures in species, might lead

to laws of change, which would then be main object of study, to guide our speculations with respect to past and future. (The grand question which every naturalist ought to have before him when dissecting a whale or classifying a mite, a fungus, or an infusorian is, "What are the Laws of Life?")

Where we have near genera far back, as well as at present time, we might expect confusion of species. Important. For instance take Valvata and Conus (??) [137] which now run together; were not both genera formerly abundant?

Seed of Ribston Pippin tree producing crab.[138] (Is [it like] the offspring of a male and female animal of one variety going back?) Whether this going back may not be owing to cross from other trees???? Do the seeds of Ribston Pippin and Golden Pippin produce real crabs, and in each case similar or mere mongrels?

It really would be worth trying to isolate some plants under glass bells and see what offspring would come from them. Ask Henslow for some plants whose seeds go back again, not a monstrous plant, but any marked variety. Strawberry produced by seeds?? Universality of generation strongly shown by hybridity of ferns, hybridity showing connexion of two plants.

Animals whom we have made our slaves we do not like to consider our equals. Do not slave holders wish to make the black man other kind? Animals with affections, imitation, fear of death, pain, sorrow for the dead, respect.

We have no more reason to expect [to find] the father of mankind, than Macrauchenia,[139] yet it may be found. We must not compare chances of embedment in man in present state with what he is as former species. His arts would not then have taken him over whole world. The soul by consent of all is superadded; animals not got it, not look forward. If we choose to let conjecture run wild, then animals our fellow brethern in pain, disease, death and suffering, and famine, our slaves in the most laborious works, our companions in our amusements; they may partake from our origin in one common ancestor; we may be all netted [140] together.

Hermaphrodite animals couple; argument for true molluscs coupling.[141]

Geograph. Journal, Vol. V, P. I, p. 67: Dr. Coulter [142] on decrease of population in California, cessation of female offspring; applicable to any animal.

Athenaeum.,[143] p. 154, 1838. Hybrid Ferns.

It may be argued against theory of changes, that if so, in approaching desert country or ascending mountains you ought to have a gradation of species; now this notoriously is not the case. You have stunted species, but not such as would make species (except perhaps in some plants and then a chain of steps is found in same mountain). How is this explained by law of small differences producing more fertile offspring? 1st. All variation of animal is either effect or adaptation, therefore animal best fitted to that country when change has taken place. Nature . . .[144]

Any change suddenly acquired is with difficulty permanently transmitted. A plant will admit of a certain quantity of change at once, but afterwards will not alter. This need not apply to very slow changes, without crossing. Now a gradual change can only be traced geologically (and then monuments imperfect) or horizontally, and then cross-breeding prevents perfect change. It is scarcely possible to get evidence of two races of plants run wild (for we know that such can take place without impregnating each other), for if they are different then they will be called species, and mere producing fertile hybrids will not destroy that evidence, as so many plants produce hybrids, or else whole fabric will be overturned. Hence extreme difficulty, argument in circle. Falkland Island case good one of animals not soon being subjected to change in Americas; perhaps merely gone back previous to fresh change. Get a good many examples of animals and plants very close (take European birds, instance Gould's case of Willow wren) and others varying in wild state to show that we do not know what amount of difference prevents breeding; or as others would express it, amount of varying in wild state.

When breaking up the primeval continent, Indian Rhinoceros, Java, and Sumatra ones, all different. Join Sumatra and Java together by elevation now in progress and you will have two Tapirs existing in East Indian seas. Marsupial animals all show greater connexion in Quadrupeds, but *plants do not follow* by any means. Ostriches, Hippotomus [*sic*] only African; American and African forms maybe in India and East Indian Islands? Monkeys different, not travellers??

Royle's[145] case of Himalayan plants; migratory birds? He told me some story of Crane from Holland!!!, in stomach, or in feathers — seeds.

Two inhabitants of the Tropics (whether one fossil or not) are related by real relationships, as well as effect of similar temperature; now those of temperate regions and tropics are only related by one connection, viz., descent. Hence far greater discordance in latter. Hence change in form. This probably explains crag[146] and miocene. The descendants left in cooling climate might change twice over, whereas those which migrated a little to the southward would merely be specifically different, if so. Now this is difficult to explain by creation, so we must suppose a multitude of small creations.

Will Dromedaries and Camels breed?

As man has not had time to form good species, so cannot the domesticated animals with him! Modern origins shown by only one species, far more than by non-embedment of remains. Agrees with non-blending of languages? Till man acquired reason he would be limited animal in range, hence probability of starting from one point. In the crag we see the process of change of those forms which have succeeded in becoming habituated to colder climate whilst others died out, or moved toward equator (or some species might then have been wanderers.) There ought to be fewer species in proportion to genera than in present seas. All the species which survive any change may undergo indefinite change (marking in their history an Eocene, Miocene, and Pliocene epoch), whilst others may die out or move southward. Therefore species must be compared to neighbouring sea. For change of species does not measure time, but physical changes (we assume like weather on long average tolerably uniform). Comparing fossils with whole world would be like in a Meteorologic table (in comparison of temperature of two countries), finding a very hot day in one; oh, we will take a day from the equator to add to the mean of the other. If the world had cooled by secular refrigeration in chief part instead of change from insular to extreme climate, Iceland would have possessed a most peculiar Flora (and north of Europe). As European forms have travelled towards Equator, so would the plants from extreme north, which according to all analogy would have been very unlike southern European ones, — "a variation played on secular refrigeration."

Experimentise on land shells in salt water, and lizards ditto. Ask Eyton to procure me some.

Get Hope[147] to give me an account of parasitic animals of beasts varying in different climates.

Those will not object to my theory, those the philosophy who soar above the pride of the savage, they perceive the superiority of man over animals, without such resorts.[148]

M. Jarred and Dumeril[149] great work on Reptiles. M. J. says some reptiles same from Maurice [Mauritius] and Madagascar, and of Good Hope. His book probably worth studying.

Wingless birds [of] S. Continents, Ostriches, Dodo, Apteryx, Penquin, Loggerheaded Duck; larger proportion of water and small[er] of land, and a few quadrupeds.

Study productions of great Fresh Water Lakes of North America.

If parasites different whilst man and his domesticated quadrupeds are not so, [then] greater faculties of change in the articulata than Vertebrata. But how does this agree with the longevity of species in Molluscs!!!

When we talk of higher orders, we should always say intellectually higher. But who with the face of the earth covered with the most beautiful savannahs and forests dare to say that intellectuality is only aim in this world . . . ?[150]

. . . of all genera (in all classes) are not a few only cosmopolitan, and in genera peculiar to any one country do not species generally affect different stations? This would be strong argument for propagation of species.

Again, is there not similarity even in quite distinct countries in same hemisphere more than in others? Are there any cases when domesticated animals separated and long interbred having great tendency to vary? Is not man thus circumstanced? Varieties of dogs in different countries a case in point. All cases like Irish and English Hare bear upon this.

Why do Van Diemen's land people require so many imported animals?

At what part of tree of life can orders like birds and animals separate, etc., etc.?

Work out Quinary system according to three elements.

How is Fauna of Van Diemen's Land and Australia . . . ?[151]

Falconer's[152] remarks on influence of climates, situations, etc., on — (242)

Smellie[153] Philos. of Zoology (842).

White[154] regular gradat. in man (1024). (Poor, trash; Lyell.)

Fleming's[155] Philosophy of Zoology. Royle[156] on Himalayan Plants.

Would it not be possible to work through all genera and see how many confined to certain countries?; so on with families.

Ask Royle about Indian cattle with humps.

To be solved: if horses sent to India and long bred in and no new ones introduced, would not change be superinduced? Why is everyone so anxious to cross animals from different quarters to prevent them taking peculiar characters? Indian Bull?

Do species of any genus as American or Indian genus inhabit different kind of localities? If so change.

The grand question: Are there races of plants run wild or nearly so, which do not intermix, any cultivated plants produced by seed? Lychnis, Flax.[157]

In production of varieties, is it not per saltum?

Islands bordering continents same type; collect cases. African Islands? How is Juan Fernandez — Humming Birds? Types of former dogs; character of Miocene Mammalia of Europe.

Mem.: Mr. Bell's[158] case of *Sub Himalayan* land emys, decidedly an Indian form of Tortoise. On other hand fresh water tortoises from Germany (where Mr. Murchison's[159] fox was found) decidedly next species to some South American kinds.

Are the closest allied species always from distant countries, as Decandelle [*sic*][160] says? (No, he only says sometimes.) We might expect disseminated species to vary a little, but such should not be general circumstance. In insects in England surely it is not; intermediate genera we might expect.

Lindley[161] Introduct.

Dict. Scien. Naturelle.[162]

Geographie Botanique, De Candoelle [*sic*].[163]

Geol. Soc.

Horae Entomologicae.[164]

Linn. Soc.

Geoff. St. Hilaire,[165] Philosophy of Zoology.

Waterhouse.[166]

NOTES AND REFERENCES

1. Darwin undoubtedly has reference to the book of his grandfather: Darwin, Erasmus. 1794-1796. *Zoonomia; or, the laws of organic life*, 2 vols. London, J. Johnson.

2. Probably: Lamarck (J. B. P. A. de Monet de). 1830. *Philosophie zoologique*. Paris.

3. Gray, John Edward. 1835. Remarks on the difficulty of distinguishing certain genera of testaceous Mollusca by their shells alone, and on the anomalies in regard to habitation observed in certain species. *Philosophical Transactions of the Royal Society of London:* 301-310.

4. Lyell referred to dispersal of plants by icebergs, or "ice-islands." Lyell, Charles. 1837. *Principles of geology*, 5th ed., vol. 3, p. 16. London, Murray.

5. Probably Candolle, Augustin Pyramus de, and K. Sprengel. 1821. *Elements of the philosophy of plants.* (Translated from the German.) Edinburgh, Blackwood.

6. Francis Darwin transcribed "immense ages" as "immersage," see: Darwin, Francis. 1898. *Life and letters of Charles Darwin*, vol. 1, p. 367. New York, Appleton.

7. Darwin undoubtedly has reference to Ehrenberg, C. G. 1837. On the origin of organic matter from simple perceptible matter and on organic molecules and atoms; together with some remarks on the power of vision of the human eye. *Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science and Learned Societies, and from Foreign Journals;* edited by R. Taylor, **1**:555-583.

8. This no doubt is Owen, Richard, author of: *Zoology of the voyage of H.M.S. Beagle, Part 1, Fossil Mammalia.* London, 1840.

9. This entire sentence is unfinished and crossed out.

10. Remainder of page 29 and first half of page 30 are missing in the notebook.

11. Bell, Thomas. 1837. *A history of British quadrupeds, including the Cetacea.* London.

12. Jenyns, Leonard. 1835. *A systematic catalogue of British vertebrate animals.* Cambridge.

13. Duperrey, Louis Isidore. 1826-30. *Voyage autour du monde, exécuté sur la Corvette du Roi La Coquille . . . pendant les années 1822-25 . . . publie . . . par L. I. D. Zoologie par Lesson et Garnot.* Paris.

14. Smith, Andrew, author of: *Illustrations of the zoology of South Africa, consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834-1836; etc.* London, 1838. Darwin visited with Smith while in Capetown, South Africa in 1836.

15. Humboldt, Alexander von. 1811. *Political essay on the Kingdom of New Spain.* Transl. from the original French, by John Black, 2 vols. New York.

16. I am not sure to what Darwin has reference here. He spells the word "monucle" in this line and "monucule" in the next. I have not found either word in such context in any other writings by Darwin or his contemporaries. Perhaps he means "monocule" and is suggesting that the progenitor of all animals was a cyclops-like creature or perhaps he means to say "molecule," as he did previously on page 249. Possibly he meant to use "minuscule," or even "monticule." See also Ehrenberg, *op. cit.*, note 7.

17. In the diagram there are 13 lines that have a perpendicular line at the end.

18. In the diagram there are 12 lines that are without a perpendicular line at the end.

19. In this and in the preceding paragraphs Darwin to all intents and purposes formulates the postulates of his theory of natural selection, viz., the survival of the fittest and the constancy of populations generation after generation.

20. Cuidado — Be careful!

21. Darwin no doubt has reference to the Quinary System of classification described by Macleay, William Sharp, in *Horae entomologicae; or, essays on the Annulose animals, etc.*, vol. 1, pts. 1, 2, London, 1819, 1821. William Swainson also described the system in *A treatise on the geography and classification of animals*, London, Longman, etc., in Lardner, D., *The Cabinet Cyclopaedia.* 1835. The system was based on the postulate that the animal kingdom may be classified into five major divisions and that these divisions have such a relation to each other that they form a circle when grouped together according to morphological similarities. Thus each division includes some taxonomic forms which bear a close resemblance through affinities or analogies to two of the other major divisions. Since each of the five major divisions is related by some of its members to two of the remaining divisions, the entire group of five must have a circular arrangement

amongst themselves. Also each of the five major divisions itself was thought to be composed of five smaller taxonomic units, each of which similarly was circularly related to two of the five units within its division.

22. Fries, Elias Magnus, author of: *Systema Mycologicum, etc.*, 3 vols., 1821-32. Fries, according to Swainson (*op. cit.*, note 21, p. 216), also suggested that taxonomic groups are arranged in circles, but in Fries' system there were four major groups instead of five.

23. Swainson, *op. cit.* note 21, p. 220, mentions Newman (Edward), author of *Sphinx Vespiformis: An Essay.* London, 1832. Newman, according to Swainson also supported the circular theory of classification, but believed the "magic" number of circles to be seven.

24. Wellsted, Lieutenant R. 1836. Observations on the coast of Arabia between Rás Mohammed and Jiddah. *Journal of the Royal Geographical Society of London,* **6**:51-96.

25. Remainder of page missing.

26. Gould, John. 1837-38. *A synopsis of the birds of Australia and the adjacent islands.* Pts. 1-4. London.

27. Van Diemen's Land is Tasmania.

28. Remainder of page missing.

29. Cuvier, G. 1827. *Essay on the theory of the earth,* 5th ed. (Translated from the French by R. Kerr.) Edinburgh, Blackwood.

30. Deshayes, Gérard Paul. 1836-37. Séance du 17 avril 1837. *Bulletin de la Société Géologique de France,* **8**:212-224.

31. This reference probably is Macculloch, John. 1831. *A system of geology, with a theory of the earth, and an explanation of its connexion with the Sacred Records,* 2 vols. London.

32. Probably Isidore Geoffroy Saint-Hilaire or René P. Lesson, or both.

33. Pages 55 and 56 missing.

34. Waterhouse, George R., author of: *Zoology of the voyage of H.M.S. Beagle, Part 2, Mammalia.* London, 1839. I could not locate a reference to a specific paper by Waterhouse to which Darwin probably refers here.

35. Heteromera is a division of beetles including darkling and blister beetles; the Chrysomelidae are leaf beetles.

36. Lyell, Charles. 1833. *Principles of geology,* vol. 3. London, Murray.

37. Pippin, a variety of apple.

38. Swainson, *op. cit.,* note 21.

39. Pages 69 and 70 missing.

40. Pages 75 and 76 missing.

41. Crossed out.

42. Probably Don, George, author of *A general system of gardening and botany.* London, 1832-1838, or possibly Don, David, both botanists, and brothers.

43. Cuvier, G. 1829-30. *Le règne animal distribué d'après son organisation, etc.,* Tomes 1-5. Paris.

44. Stonesfield slate, a geological formation of the Jurassic. See Lyell, Charles. 1850. *Principles of geology,* 8th ed. p. 143. London, Murray. See also Lylell, *op. cit.,* note 4 (in vol. 1, p. 237).

45. Kotzebue, Otto von. 1821. *A voyage of discovery, into the South Sea and Beering's Straits, for the purpose of exploring a North-East passage . . . in . . . 1815-1818.* (Remarks and opinions of the Naturalist of the Expedition, A. von Chamisso, vol. 2) 3 vols. London.

46. Richardson, John. 1829-37. *Fauna Boreali-Americana; or the zoology of the northern parts of British America.* 3 vols. London.

47. Humboldt, F. H. Alexander von, and Aimé Bonpland. 1807. *Voyage de Humboldt et Bonpland. Part 5. Essai sur la géographie des plantes, accompagné d'un tableau physique des régions équinoxiales . . . Rédigé par A. de Humboldt.* Paris.

48. Swainson, *op. cit.,* note 21.

49. Brown, Robert. 1831. General view of the botany of the vicinity of Swan River. *Journal of the Royal Geographical Society of London,* **1**:17-21.

50. Geoffroy Saint-Hilaire. 1837. Singe fossile de Sansan. *L'Institut, Journal des Académies et Sociétés Scientifiques de la France et de l'Étranger,* Paris, **5**:242-244.

51. "singe," ape or monkey.

52. *Colobus,* a genus of African monkey.

53. Semnopitheque, a name now technically invalid for the Old World langur monkeys.

54. Sapajou, a monkey of the genus *Cebus* of S. America.

55. See Lyell, *op. cit.*, note 4 (in vol. 2, p. 402).

56. *Muscicapa coronata?* Lath., a tyrant-flycatcher of the Galapagos Islands. See Darwin, Charles, 1839. *Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle*, p. 461. London, Colburn.

57. This word is crossed out, but looks as if it might have been "Chat" or "Chais." Perhaps Darwin meant "Calandria" a mocking-bird of Patagonia. See Darwin, *op. cit.*, note 56, pp. 62-63, where *Orpheus modulator* and *O. Patagonica* D'Orbigny are mentioned; see also p. 475, where various species of the Galapagos' *Orpheus* are mentioned. Possibly Darwin intended to write "Chatham" for Chatham Island.

58. Perhaps this should read, "when points are finally gained, if any, then the facts become connected."

59. Pages 107 and 108 missing.

60. Geoffroy Saint-Hilaire, Étienne, 1830. *Principes de philosophie zoologique, discutés en Mars 1830 au sein de l'Académie Royale des Sciences.* Paris.

61. *Op. cit.*, note 60.

62. *Op. cit.*, note 60.

63. *Op. cit.*, note 60.

64. Geoffroy Saint-Hilaire, Étienne, 1818. *Philosophie anatomique.* Paris.

65. The words "different animals" are crossed out.

66. Sternberg, Count, 1827. On the distribution of living and fossil plants. *Edinburgh New Philosophical Journal*, April to October: 190-192.

67. Cuvier, Frédéric. 1827-28. Essay on the domestication of mammiferous animals, with some introductory considerations on the various states in which we may study their actions. *Edinburgh New Philosophical Journal*, October to April: 45-60; 292-297.

68. The correct quotation is "concurrence."

69. Darwin, apparently inadvertently, omitted this portion of the quotation.

70. Crawford. 1827. Account of Mr. Crawford's mission to Ava. *Edinburgh New Philosophical Journal,* April to October: 359-370.

71. Park, Thomas. 1827-28. Mr. Thomas Park's journey into the interior of Africa. *Edinburgh New Philosophical Journal,* October to April: 410.

72. Pages 123 through 128 missing.

73. Probably has reference to Macleay, *op. cit.,* note 21, who discussed analogy and affinity.

74. Thus the wings of birds and bats are related to the air.

75. Monteith, Colonel (William), E. I. C. 1833. Journal of a tour through Azerdbijan and the shores of the Caspian. *Journal of the Royal Geographical Society of London,* **3**:1-58.

76. Hilhouse, William. 1834. Journal of a voyage up the Massaroony in 1831. *Journal of the Royal Geographical Society of London,* **4**:25-40.

77. Campbell, Major (James). 1834. Geographical memoir of Melville Island and Port Essington, on the Cobourg Peninsula, Northern Australia; with some observations on the settlements which have been established on the north coast of New Holland. *Journal of the Royal Geographical Society of London,* **4**:129-181.

78. *Op. cit.,* note 50.

79. Undoubtedly Geoffroy Saint-Hilaire, *op. cit.,* note 50.

80. Baer. 1837. Aurochs du Caucase. *L'Institut, Journal des Académies et Sociétés Scientifiques de la France et de l'Étranger,* Paris, **5**:260-261.

81. Sir Francis Sacheverel Darwin (1786-1859). For biographical notes, see Pearson, Karl. 1914. *The life, letters and labours of Francis Galton,* vol. 1:22-25. Cambridge Univ. Press.

82. See Darwin, *op. cit.,* note 56 (p. 163 in Darwin).

83. Yarrell, William, author of numerous papers including: On the laws which regulate the change of plumage in birds. *Transactions of the Zoological Society of London,* **1**:13-20, 1835.

84. Eyton, Thomas C. 1837. Some remarks upon the theory of hybridity. *Magazine of Natural History, and Journal of Zoology, Botany, Mineralogy, Geology, and Meteorology,* London, **1**:357-359. Conducted by J. C. Loudon.

85. Gould, John. 1837. Observations on some species of the genus *Motacilla* of Linnaeus. *Magazine of Natural History, and Journal of Zoology, Botany, Mineralogy, Geology, and Meteorology, London,* **1**:459-461. Conducted by J. C. Loudon.

86. Westwood, J. O. 1837. On *Diopsis,* a genus of dipterous insects, with descriptions of twenty-one species. *Transactions of the Linnean Society of London,* **17**:283-314.

87. I could find no reference to Wynne in the published literature.

88. Undoubtedly Lord Powis. See Darwin, Charles. 1868. *Variation of animals and plants under domestication,* vol. 1, p. 83; vol. 2, p. 45. London, Murray.

89. Darwin's cousin, William Darwin Fox.

90. Kirby, William. 1835. *On the power, wisdom and goodness of God as manifested in the creation of animals and in their history, habits and instincts,* 2 vols. London, William Pickering. (Bridgewater Treatises.)

91. Humboldt, Alexander de, and Aimé Bonpland. 1821. *Personal narrative of travels to the equinoctial regions of the New Continent during the years 1799-1804.* Vol. 5, pt. 2. (Transl. by Williams) London, Longman, etc.

92. Kirby, *op. cit.*, note 90.

93. Cline, Henry. 1805. *On the form of animals.* London.

94. Buckland, William. 1836. *Geology and mineralogy considered with reference to natural theology.* London, William Pickering. (Bridgewater Treatises.)

95. Brongniart, Ad. 1837. Végétaux fossiles. *L'Institut, Journal des Académies et Sociétés Scientifiques de la France et de l'Étranger,* Paris, **5**:318-321.

96. Pages 151 through 154 missing in the notebook. The reference is: Ehrenberg. 1837. Infusoires fossiles du tripoli d'Oran. *L'Institut, Journal des Académies et Sociétés Scientifiques de la France et de l'Étranger,* Paris, **5**:330-331.

97. Buch, Leopold von. 1836. *Description physique des Îles Canaries, suivie d'une indication des principaux volcans du globe.* Traduite de l'Allemand par C. Boulanger. Revue et augmentée par l'auteur. Paris, Levrault.

98. Humboldt, F. H. Alexander von. 1817. *De distributione geographica plantarum secundum coeli temperiem et altitudinem montium, prolegomena.* Lutetiae Parisiorum.

99. Lyell, *op. cit.*, note 4 (p. 367 in Lyell).

100. Pages 159 and 160 missing.

101. Probably Richard Owen.

102. Undoubtedly John Hunter. For various references, see Abernethy, J. 1817. *Physiological lectures exhibiting a general view of Mr. Hunter's physiology and of his researches in comparative anatomy, etc.;* Hunter, John. 1835-37. *The works of John Hunter. With notes.* Edited by J. F. Palmer. 4 vols. London.

103. Eyton, Thomas C. 1837. Notice of some osteological peculiarities in different skeletons of the genus *Sus. Proceedings of the Zoological Society of London,* Part 5:23-24.

104. See note 34.

105. This reference possibly is one of the following: Ogilby, W. 1833. Characters of a new genus of carnivorous Mammalia (*Cynictis*), from the collection of Mr. Steedman. *Proceedings of the Zoological Society of London,* Part 1:48-49; Ogilby, W. 1836. Remarks upon the probable identity of *Cynictis melanurus* Mart., with a species noted by Boshman under the name of Kokebog. *Proceedings of the Zoological Society of London,* Part 4:56.

106. Serres. 1837. Anatomie des mollusques. *L'Institut, Journal des Académies et Sociétés Scientifiques de la France et de l'Étranger,* Paris, **5**:370-371.

107. Pages 165 and 166 missing from the notebook. The reference undoubtedly is Horsfield, Thomas, author of several articles including: Notice of a species of *Ursus* (*U. isabellinus*) from Nepal. *Transactions of the Linnean Society of London,* **15**:332-334, 1827.

108. I could find no such specific reference, see however Smith, *op. cit.*, note 14.

109. Phillips, John. 1837. *A treatise on geology.* London, Longman, etc., in Lardner, D. *The Cabinet Cyclopaedia, etc.,* vol. 1.

110. Wealden, a freshwater geological formation underlying the Lower Cretaceous in England. See Lyell, *op. cit.*, note 4 (vol. 4:302 in Lyell).

111. Pages 173 and 174 missing.

112. For further citations on Aston in the literature see: Pearson, Hesketh. 1930. *Doctor Darwin* (p. 180). London, Dent and Sons; Oswald, Arthur. 1953. Aston Hall, Warwickshire — I. The property of the Corporation of Birmingham. *County Life*, London, **114**:552-555, 620-623, 694-697; *Historic Houses and Castles in Great Britain and Northern Ireland* (1959 Edition), Index Publishers Limited, London, 1959.

113. Pages 177-178 missing.

114. Deshayes, Gérard Paul. 1833-1834. Mémoires et communications séance du 3 février 1834. *Bulletin de la Société Géologique de France*, **4**:200-293.

115. I have not been able to find any bibliographic reference to Mr. McClay. Undoubtedly should be Macleay (see note 21).

116. Dr. Andrew Smith, *op. cit.*, note 14.

117. Herbert, William. 1822. On the production of hybrid vegetables; with the result of many experiments made in the investigation of the subject. *Transactions of the Horticultural Society of London*, **4**:15-50. In this article Herbert proposes that new species are formed by divergence and hybridization.

118. Morton, George. 1821. A singular fact in natural history. (Peculiarities of the progeny of an Arab horse from a mare that had previously bred with a Quagge.) *Philosophical Transactions of the Royal Society of London:* 20-23.

119. Pages 185 through 190 missing. "Folds" no doubt should be "foals."

120. Herbert, William. 1820. Instructions for the treatment of the Amaryllis longifolia, as a hardy aquatic, with some observations on the production of hybrid plants, and the treatment of the bulbs of the genera Crinum and Amaryllis. *Transactions of the Horticultural Society of London*, **3**:187-196. An interesting quotation from p. 196 of this article is the following: "Considering the wide field that is open for the creation of new species of plants, by hybrid intermixture, some mode of naming them must be adopted, or the art of cultivators will break down all the landmarks of the botanist." See also Herbert, William. 1837. *Amaryllidaceae; preceded by an attempt to arrange the monocotyledonous orders, and followed by a treatise on cross-bred vegetables, etc.* London.

121. Darwin probably was referring to either George Don or David Don, and not Donn. See note 42.

122. Carmichael, Dugald. 1818. Some account of the island of Tristan da Cunha and its natural productions. *Transactions of the Linnean Society of London,* **12**:483-513.

123. Probably Ellis, William. 1829. *Polynesian researches, during a residence of nearly six years in the South Sea Islands, etc.* 2 vols., London.

124. The word "planet" was inserted in brackets by Darwin, Francis, *op. cit.,* note 6 (p. 370 in Darwin).

125. Pages 197 through 202 missing.

126. Lowe, R. T. 1833. Primitiae Faunae et Florae Maderae et Portus-Sancti; sive species quaedam novae vel hactenus minus rite cognitae animalium et plantarum in his insulis degentium breviter descriptae. *Transactions of the Cambridge Philosophical Society,* **4**:1-70.

127. The most nearly appropriate bibliographic references that I could find are: Laurillard, Charles Léopold, Valenciennes and Pentland. 1835? *Catalogue des préparations anatomiques laissées dans le Cabinet d'Anatomie comparée du Muséum d'Histoire Naturelle,* par G. Cuvier. (Paris?); and Darwin, *op. cit.,* note 56 (p. 153 in Darwin).

128. Pages 209 and 210 missing.

129. *Op. cit.,* notes 84 and 103.

130. I believe Darwin means that under his theory two distinct species would not independently evolve into a single species.

131. Bell, *op. cit.,* note 11.

132. See note 44. The correct spelling should be "Stonesfield."

133. *Op. cit.,* note 123. See also Williams, John. 1837. *Narrative of Missionary enterprises in the South Sea Islands; with remarks upon the natural history . . . etc.* London.

134. See Duperrey, *op. cit.,* note 13.

135. This sentence crossed out.

136. Oolite, or Jura Limestone Group. See Lyell, *op. cit.,* note 4 (vol. 4, p. 303 in Lyell).

137. *Valvata,* a genus of freshwater snails; *Conus,* a genus of marine snails.

138. Probably the Ribston Pippin apple occasionally produced a crab apple.

139. *Macrauchenia,* an extinct three-toed, long-necked ungulate of the South American Pleistocene.

140. Francis Darwin transcribed this word as "melted" rather than "netted," *op. cit.,* note 6 (p. 368 in Darwin).

141. Pages 233 and 234 missing.

142. Coulter, Thomas. 1835. Notes on upper California. *Journal of the Royal Geographical Society of London,* **5**:59-70.

143. Martens, M. 1838. On hybridity in ferns. *Athenaeum Journal of English and Foreign Literature, Science and the Fine Arts,* no. 539: 154. London.

144. Pages 237 and 238 missing.

145. Royle, John Forbes. 1835. Illustrations of the botany and other branches of the natural history of the Himalayan Mountains, and of the flora of Cashmere. *Journal of the Royal Geographical Society of London,* **5**:361-655.

146. Crag, a geological formation of the Pliocene of England. See Lyell, *op. cit.,* note 4 (vol. 4, pp. 71-72 in Lyell).

147. Probably Hope, Frederick W., author of: Descriptions of some species of Carabidae, collected by Charles Darwin, Esq. in his late voyage. *Transactions of the Entomological Society of London,* **2**:128-130, 1837-40.

148. Pages 249 and 250 missing.

149. "M. Jarred" is crossed out. Perhaps Darwin confused Jarred with Gérard of Gérard Paul Deshayes in: Bélanger, Charles. 1834. *Voyage aux Indes-Orientales, . . . les îles de Java, de Maurice etc., . . . Zoologie,* par M.M. Bélanger, I. Geoffroy Saint-Hilaire, Lesson, Valenciennes, Deshayes et Guérin. Paris. The reference to Duméril is probably: Duméril, André Marie Constant and Gabriel Bibron. 1834-54. *Erpétologie générale; ou, histoire naturelle complète des reptiles.* Paris, Roret.

150. Pages 253 through 260 missing.

151. The remainder of this and the next page blank in the notebook, and pages 266-271 missing.

152. Falconer, Hugh, author of numerous zoological and botanical papers. See: *Catalogue of scientific papers (1800-1863).* Royal Society of London, 6 vols. London, Eyre, etc. 1867-1872.

153. Smellie, William. 1790-99. *The philosophy of natural history.* 2 vols. Edinburgh.

154. White, Charles. 1799. *An account of the regular gradation in man, and in different animals and vegetables; and from the former to the latter.* London.

155. Fleming, John. 1822. *The philosophy of zoology; or a general view of the structure, functions, and classification of animals, etc.* 2 vols. Edinburgh.

156. Royle, *op. cit.*, note 145.

157. Pages 276 and 277 missing.

158. Bell, Thomas. 1828. On *Hydrapsis,* a new genus of freshwater tortoises, of the family Emydidae. *Zoological Journal;* by Thomas Bell, etc., London, **3**:511-513.

159. Murchison, Roderick Impey. 1835. On the fossil fox of Oeningen, with an account of the lacustrine deposit in which it was found. *Transactions of the Geological Society of London.* **3**:277-290.

160. Candolle, Alphonse de. 1834. Fragment d'un discours sur la Géographie Botanique. *Bibliothèque Universelle des Sciences, Belles Lettres, et Arts, etc.,* Genève. **56**:1-29.

161. Lindley, John. 1830. *An introduction to the . . . natural system of Botany, or a systematic view of the organisation . . . of the whole vegetable kingdom, etc.,* London.

162. *Dictionnaire des sciences naturelles, etc.* Par plusiers professeurs, etc., . . . Strasbourg, Levrault; Paris, Le Normant, 1816-30. (M. F. Cuvier est chargé . . .)

163. Candolle, *op. cit.*, note 160.

164. *Horae entomologicae, op. cit.*, note 21.

165. Geoffroy Saint-Hilaire, *op. cit.*, note 60.

166. Waterhouse, *op. cit.*, note 34.

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SKELETON AND MUSCULATURE OF THE THORAX OF *GELASTOCORIS OCULATUS* (FABRICIUS) (HEMIPTERA-HETEROPTERA)

By MARGARET C. PARSONS
Harvard Biological Laboratories

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
MAY, 1960

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No. 7 — *Skeleton and Musculature of the Thorax of Gelastocoris oculatus (Fabricius) (Hemiptera-Heteroptera)*

By Margaret C. Parsons

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INTRODUCTION

The members of the family Gelastocoridae are predaceous, littoral insects which live in swamps or along the shores of ponds and streams. The family is comprised of only two genera, *Gelastocoris* and *Nertha*. They are commonly called "toad bugs" because of their jerky, hopping means of locomotion, their roughened exoskeleton, and their prominent, laterally projecting compound eyes.

In a previous paper (Parsons, 1959) the author has described the cephalic skeleton and musculature of *Gelastocoris oculatus*. The study of the anatomy of this insect was undertaken for two reasons. First, except for those characters which are of taxonomic interest, almost nothing was known of the morphology of the Gelastocoridae. The few earlier works on the biology and taxonomy of this family are briefly reviewed in my previous paper.

Secondly, the Gelastocoridae, along with the closely related shore-dwelling families Ochteridae and Saldidae, occupy a basic position in previous theories of the evolution of the aquatic and semi-aquatic Heteroptera. These families are generally believed to represent an intermediate stage in the evolution of the water bugs from terrestrial forms. The various phylogenetic schemes which have been proposed have been based upon relatively few anatomical features, most, if not all, of which are external. It appeared, therefore, that a thorough study of both the external and internal morphology of one of the littoral Heteroptera might reveal additional evidence which could clarify the phylogenetic position of this group. *Gelastocoris* was used for this study because it could be obtained in large numbers and because it proved to be an excellent, easily kept laboratory animal.

The present study was greatly facilitated by the previous work of Larsén. That author has published many excellent papers on the thorax of the Heteroptera, and the two works (1945a and b) in which he described and compared in detail the thoracic skeleton and musculature of representatives of a great many different families are especially helpful. Previous to Larsén's studies there were very few works on the heteropteran thorax. Tower (1913) described briefly the external appearance of the thorax in *Anasa*, and Taylor (1918) discussed the thoracic sclerites of several families of Heteroptera, but included little detail. Hamilton (1931) studied the skeleton and musculature of the thorax of *Nepa* rather superficially. A much more extensive description of the skeleton and musculature was given by Malouf (1933) in his well illustrated paper on the thorax of *Nezara*. Rawat (1939) also briefly described both the muscles and the sclerites of this region in *Naucoris*. More recently Griffith (1945) and Esaki and Miyamoto (1955) have described the thoracic skeletons of *Ramphocorixa* and the Veliidae respectively. Three other studies have been made which include both the skeleton and the musculature; these are the works of Sprague (1956) on *Hydrometra*, Akbar (1957) on *Leptocorisa*, and Lauck (1959) on *Lethocerus*. The latter study is particularly valuable for its brief but thorough description of the musculature.

The author is indebted to Mr. Edwin P. Marks, of Washburn University, and to the members of the C. V. Riley Entomological

Society, of Columbia, Missouri, who provided the insects used in the present study. I also wish to thank Professor Frank M. Carpenter and my husband, Dr. Thomas S. Parsons, both of Harvard University, for their helpful advice and for their critical examination of the manuscript. This study was carried out during the tenure of the Ellen C. Sabin Fellowship, awarded by the American Association of University Women.

Figure 1. Dorsal view of *Gelastocoris oculatus*, legs removed. About 11X.

MATERIALS AND METHODS

Since *Gelastocoris* is a fairly large insect (approximately 6 to 8 mm. long), the skeleton and musculature could be studied by means of dissection under a stereoscopic microscope. Most of the dissections were made upon insects preserved in alcoholic

Bouin's solution, 10 per cent formalin, or Kahle's solution, and stored in 70 per cent alcohol. Since fresh material was sometimes needed, live gelastocorids were kept in the laboratory. The conditions under which they were kept have been described in a previous paper (Parsons, 1959).

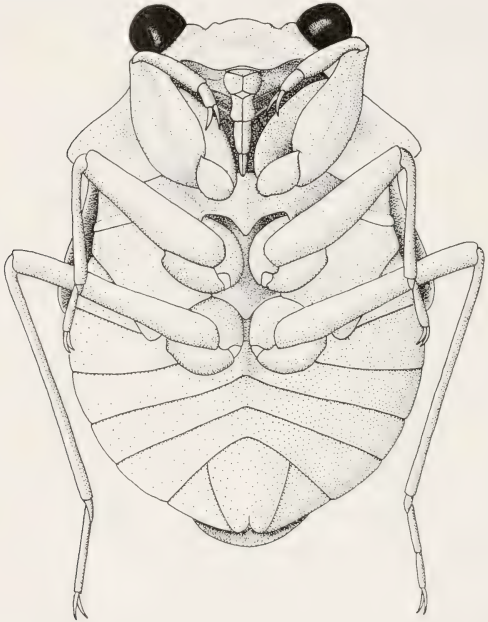


Figure 2. Ventral view of *G. oculatus* female, spines and hairs of legs omitted.

SKELETON

Prothorax

Cervical region. The cervical region of *Gelastocoris* is relatively simple. A *cervical membrane* (*CM*), devoid of cervical sclerites, connects the postocciput of the head with the inturned anterior

margin of the prothorax (Fig. 5). The latter forms a tight collar around the postocciput. Two short tendons extend from the middorsal region of the cervical membrane into the thorax. From the posterior margin of the postocciput, two pairs of apodemes project into the thorax, providing points of attachment for muscles. The longer of these, the *occipital condyles* (*O*), extends dorsally from the ventrolateral regions of the postocciput. Dorsal to them are the much shorter *lateral apodemes* (*L*), which project posteroventrally.

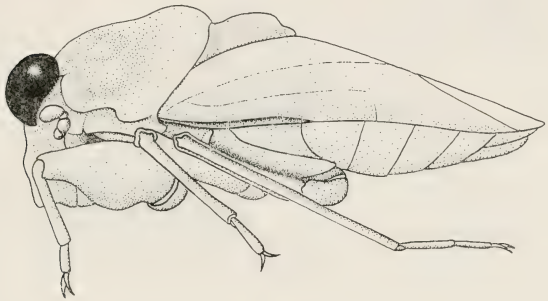


Figure 3. Lateral view of *G. oculatus* female.

Tergum. The prothoracic tergum is a large plate covering much of the anterior half of the body dorsally (Fig. 1). Much of its area is due to marginal evaginations, and the actual prothoracic cavity is comparatively small. These evaginations produce lobes which overlap the postocciput anteriorly and the mesonotum posteriorly. They are especially pronounced along the posterior and posterolateral tergal margins, where they form a broad *posterior protergal lobe* (*LP*) (the "tergal flap" of Malouf, 1933, and the "Hinterlappen" of Larsén, 1945a and b) shielding the anterior part of the mesonotum. The anterolateral lobes of the protergum are concave anteriorly, conforming to the shape of the head at the bases of the compound eyes. The two walls of all these marginal evaginations are fused together and appear as a single layer. A pronounced *transverse ridge*

(*TR*) ("Querleiste" of Larsén, 1945a and b) marks the anterior border of the posterior lobe and the posterior limit of the prothoracic cavity (Figs. 5 and 6). This ridge is a continuation of the ventral layer of the posterior lobe; attached to it is the intersegmental membrane (*I*) joining the prothorax to the mesothorax.

Pleuron. The boundary between the pleuron and the marginal tergal evaginations is not clear externally. A short *pleural suture* (Fig. 4, *PS*) separates the small *episternum* (*ES*) from the larger *epimeron* (*EP*). The ventral regions of each of these are evaginated to form *supracoxal lobes* (*EPS* and *ESS*) ("epimeral and

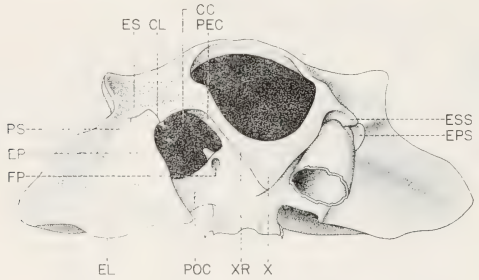


Figure 4. Ventral view of the prothorax, tilted slightly to the left. The muscles and the right leg have been removed; the left leg is cut off near the distal end of the coxa.

episternal flaps" of Malouf, 1933, and Akbar, 1957; "Supracoxallappen" of Larsén, 1945a and b) overlapping the bases of the *coxae*. The episternal and epimeral supracoxal lobes are separated by a pronounced *coxal cleft* (*CL*), which extends dorsally to the *coxal process* (to be described below). Externally the coxal cleft appears to be a ventral extension of the pleural suture; internally the cleft and the suture are separated by the coxal process. The posterior margin of the epimeron forms a large *posterior epimeral lobe* (*EL*) (the "lateral epimeral flap" of Malouf, 1933), which covers much of the mesothoracic epimeron as well as the bases of the forewings (Figs. 4, 5, and 6). Laterally, this lobe is continuous with the posterior lobe of the protergum,

the point of junction being braced by a U-shaped sclerotized strut (Fig. 5, *ST*). The anterior margin of the inner wall of the epimeral lobe is turned dorsally to form the ventral part of the transverse ridge, which medially becomes quite low and continues into the *posterior sternal process* (to be described below) (Fig. 6).

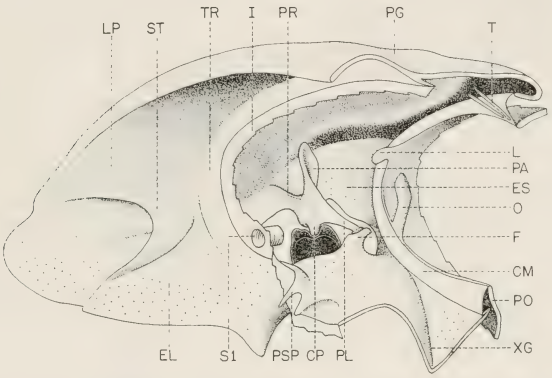


Figure 5. Posteromedial view of the left half of the prothorax and of the postoccipital region of the head. The tendons of the pericoxal membrane and the muscles have been removed.

The large *coxal cavity* (*CC*) is bordered laterally by the epimeron and episternum and medially by the sternum (Fig. 4). Anterior to the coxal cavity the episternum meets the sternum, forming a narrow *precoxal bridge* (*PEC*); posteriorly the fused epimeron and a sternum form a broad *postcoxal bridge* (*POC*). There is no clear boundary between the sternal and pleural elements. A view of the inner surface of the pleuron (Figs. 5 and 6) shows that the short pleural suture produces a distinct *pleural ridge* (*PR*) internally. At the end of the ridge is a strong *coxal process* (*CP*) ("coxal articulation" of Griffith, 1945; "Hüftgelenkkopf" of Larsén, 1945 a and b; "pleural articular process" of Akbar, 1957) which projects a short distance into the coxal cavity

and articulates with the base of the coxa. Just dorsal to the coxal process is a large, lamellar *pleural apophysis* (*PA*) ("pleural arm" of many authors; "Pleuralhaken" of Larsén, 1945a and b) which extends dorsally nearly to the lateral part of the notum. It does not fuse with the latter, as it does in many water bugs. A thick membrane (Fig. 5, *PL*) projects medially from the pleural apophysis to the *furca* (to be described below). A similar connection between the prothoracic pleural apophysis

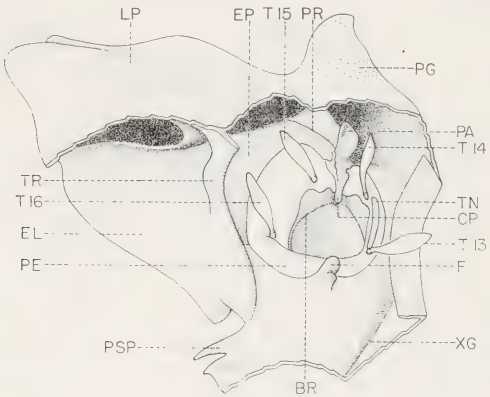


Figure 6. Dorsomedial view of the left half of the prothorax. The muscles and the pleurosternal bridge have been removed, and much of the medial part of the protergum has been cut away.

and the furca has been described in *Corixa* and *Salda* by Larsén (1945a and b), and in *Ramphocorixa* by Griffith (1945); the latter author termed it the *pleurosternal bridge*, and that term will be used here.

Sternum. The anterior part of the sternum is produced into a large triangular process which lies between the coxae (Fig. 4, *X*). A similar process in the metathorax of Heteroptera has been termed the *xiphus* by many authors, and that term will be used for this prothoracic structure. Along the posteroventral edge of

the xiphus runs a sharp, V-shaped ridge (Fig. 4, *XR*) which produces a groove internally (Figs. 5 and 6, *XG*). Laterally this ridge, which will here be called the *xiphal ridge*, continues into the precoxal bridge and runs along the posterior edge of the supracoxal lobe of the episternum, ending at the coxal cleft. The xiphal ridge corresponds to the "external ridge of the basisternum" of Akbar (1957); since it does not pass through the bases of the furcae, it probably does not represent a sternacostal suture. Akbar (1957) found a sternacostal suture posterior to this ridge in the prothorax of *Nezara;* in *Gelastocoris* there is no visible prothoracic sternacostal suture.

Just medial to the coxal cavities, on either side of the midline, are the short, thick sternal apophyses or *furcae* ("anterior endosternites" of Rawat, 1939; "Furcaäste" of Larsén, 1945a and b) (Figs. 5 and 6, *F*). Externally their positions are marked by the *furcal pits* (Fig. 4, *FP*). As Larsén (1945b) has pointed out, the term "furcal branch" is preferable to that of "furca" in the Heteroptera, since the furca is a single medial structure in many higher insects; the paired apophyses of the Heteroptera probably represent the branches of the single furca of other insects. For convenience, however, the term "furca" will be used here. The prothoracic furcae of *Gelastocoris* are each subdivided into a lateral and a medial arm.

The posterior part of the sternum projects into the cavity of the mesothorax as a broad plate. Lateral to this plate are two prong-like *posterior sternal processes* (*PSP*), which are continuous with the ventral part of the transverse ridge (Figs. 5 and 6). In some specimens these processes are heavily sclerotized, while in others they appear to be more or less membranous. They may represent the "posterior horn-like processes" or "spina" of Akbar (1957), and the "posterior prothoracic endosternites" of Rawat (1939). Lauck (1959), like Rawat, believed them to be part of the furcae. Both Akbar (1957) and Larsén (1945b), however, considered them to represent the spina of other insects; the latter author observed these processes in several aquatic and terrestrial Heteroptera. Just lateral to the posterior sternal processes, in the intersegmental membrane between the prothorax and mesothorax, lies the large *first thoracic spiracle* (Fig. 5. *S1*).

Pterothorax

The mesothorax and metathorax, unlike the prothorax and mesothorax, are bound closely together, the intersegmental membrane being either very narrow or, more commonly, entirely absent. In the following discussion the two segments will be considered together.

tergum

Mesothorax. On the anteromedial portion of the mesothoracic tergum is the semicircular *first phragma* (Figs. 7 and 10, *P1*) ("prephragma" of Akbar, 1957), an invagination which extends

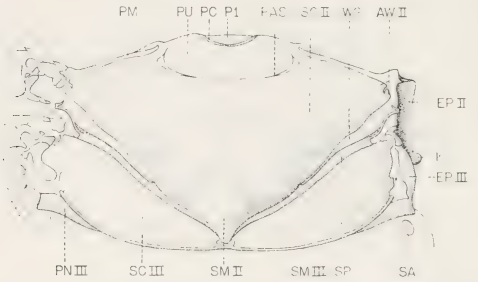


Figure 7. Dorsal view of the pterothorax. The wings have been removed from the right side, and the wings of the left side have been extended and cut off near their bases.

anteroventrally into the thoracic cavity. The two thin layers of the invagination are closely apposed, the intersegmental membrane from the prothorax attaching along the posterior edge of the more dorsal layer (Fig. 10). A narrow sclerotized *precosta* (*PC*) is present where the membrane meets the margin of the phragma, and medially two slender tendons extend anteriorly from the ventral surface of the membrane (Fig. 7).

Posterior and lateral to the first phragma lies the *mesonotum*. A broadly U-shaped *parapsidal suture* (Figs. 7 and 10, *PAS*) ("parapside" of Malouf, 1933; "pre-scutal suture" of Rawat, 1939; "convergent suture" of Lauck, 1959) separates an anteromedial *prescutum* (*PU*) ("scutum" of Malouf, 1933, and Lauck,

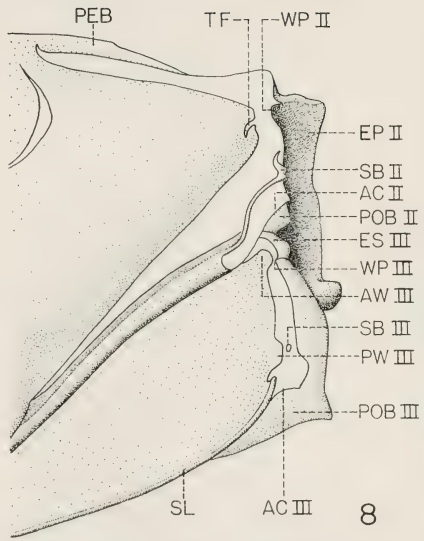


Figure 8. Dorsal view of the right side of the pterothorax. The wings have been removed.

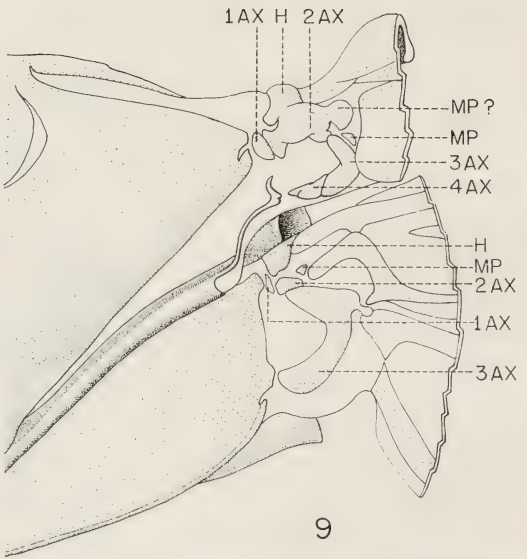


Figure 9. Dorsal view of the right side of the pterothorax. The wings have been extended and cut off near their bases.

1959) from the rest of the mesonotum. The anterolateral margins of the prescutum are connected anteriorly to the mesothoracic *episternum* by the *prealar bridges* (Fig. 10, *PEB*), which are roughly V-shaped. The parapsidal suture ends just posterior to the prealar bridges; internally it produces a very low *parapsidal ridge* (Fig. 12, *PAR*). Medial to the parapsidal suture is a narrow membranous area which is most conspicuous laterally.

The rest of the mesonotum is made up of the *scutum* (*SC*) and *scutellum* (*SM*). No scutoscutellar suture is present to separate these regions; their boundaries can be determined only by the

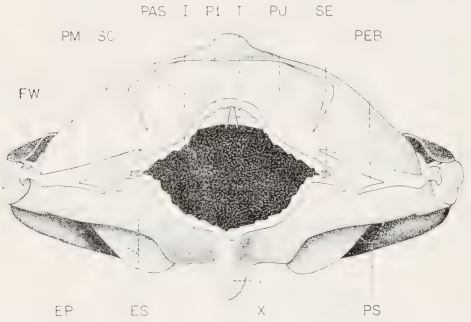


Figure 10. View of the anterior surface of the mesothorax.

insertions of the tergal muscles, which, according to Snodgrass (1927) arise only from the prescutellar area. According to this criterion, the scutellum is very narrow laterally but becomes wider medially. The scutum is bordered anteriorly by the parapsidal suture and by the *prealar membrane* (*PM*), which extends from the lateral edge of the prealar bridge into the membrane of the forewing (Figs. 7 and 10). Laterally, the scutum extends to the bases of the forewings on either side. Where it articulates with the base of the wing it is cleft by a posteriorly curved *tergal fissure* (Fig. 8, *TF*) ("Tergalspalt" of Larsén, 1945a and b). This fissure separates two small processes which together form the *anterior notal wing process* (Fig. 7, *AWII*) ("anterior wing

process" of Rawat, 1939). The more anterior process has been termed the "vectis dorsualis anterior" (Malouf, 1933), the "vorderen Tergalhebel" (Larsén, 1945a) and the "anterior notal wing process" (Akbar, 1957), while the more posterior process has been called the "vectis dorsualis posterior" (Malouf, 1933) and the "hinteren Tergalhebel" (Larsén, 1945a).

The scutellum ("scutoscutellum" of Lauck, 1959) is the posterior region of the mesonotum, which medially covers much of the metatergum. Since the latter is concealed by the forewings and since the anterior part of the mesoscutum is overlapped by the posterior lobe of the pronotum, only the mesoscutellum and the posterior part of the mesoscutum are normally visible dorsally (Fig. 1). The posterior apex of the scutellum has been termed the "scutellar flap" (Malouf, 1933) or the "Scutellarlappen" (Larsén, 1945 a and b). Along the posterior part of the scutellum runs a deep *wing groove* (Fig. 7, *WG*) which receives the posterior margin of the forewing when the latter is at rest. Medially the wing groove is narrow and sclerotized, resembling a deep suture, but laterally it becomes wider and membranous, the membrane continuing into the forewing (this membranous part of the groove corresponds to the region labelled "X" in Fig. 3B of Rawat, 1939). The posterior wall of the wing groove, along with the narrow region of the scutellum posterior to it, forms the *scutellar process* (*SP*) ("processus scutellaris tertius alae" of Malouf, 1933; "narrow sclerotized strip" of Rawat, 1939; "Scutellumfortsatz" of Larsén, 1945a and b; "lateral scutellar plate" of Akbar, 1957; probably the "frenum" of Tower, 1913). The surface of the scutellar process is somewhat lower than that of the scutellum proper. Laterally it narrows and bends anteriorly, becoming fused with the *subalare* (Fig. 8, *SBII*), an irregularly shaped sclerite lying in the posterior part of the base of the wing. Just behind the subalare is the *axillary cord* (*ACII*), which comes off from the scutellar process. Both Rawat (1939) and Akbar (1957) considered the lateral limit of the scutellar process to represent a posterior notal wing process. Larsén (1945b), however, claimed that the Heteroptera lack a posterior notal wing process, the wing instead articulating with the subalare; this is certainly the case in the mesothorax of *Gelastocoris*.

The *postnotum* ("pseudonotum" or "postscutellum" of many authors) is externally visible only laterally (Fig. 11, *PNII*). This lateral portion (the "Lateropostnota" of Larsén, 1945a and b) lies posteroventral to the subalare and axillary cord, and is continuous with the mesothoracic epimeron, forming the *postalar bridge* (Fig. 8, *POBII*) ("Postalare" of Taylor, 1918). The posterior margin of the postalar bridge is joined to the anterior edge of the metathoracic episternum, the boundary between the two being indistinct in many specimens. Medially the postnotum is concealed by the scutellar process, and the boundary between these two regions is also indistinct. A view of the inner surface

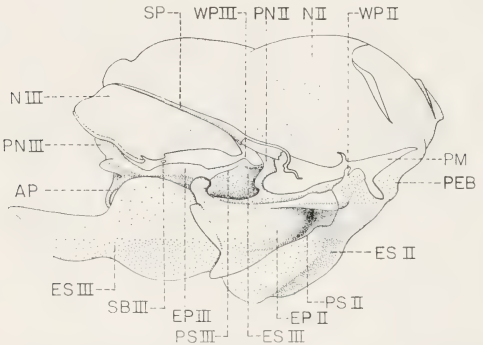


Figure 11. Lateral view of the right side of the pterothorax. The wings and legs have been removed.

of the tergum (Fig. 12) reveals that the medial part of the postnotum is extremely narrow. Posteriorly it becomes continuous with the anterior wall of the *second phragma* (*P2*) ("mesopostphragma" of Akbar, 1957), an invagination of the tergum between the mesothorax and metathorax. This is the largest of the three thoracic phragmata. Laterally it is a fairly low ridge which meets the pleuron at the boundary between the mesothoracic epimeron and the metathoracic episternum; medially it becomes much higher, and possesses, on either side of the midline, a *ventral*

process (V) ("ventrale Fortsatz of Larsén, 1945a and b). This process extends ventrally nearly to the mesosternal *furca* (*FII*) (to be described below); its two walls are not closely apposed and may be easily separated.

Metathorax. The metathoracic tergum is considerably shorter than the tergum of the preceding segment. This is true of most Heteroptera, since the main flight muscles are located in the mesothorax (Larsén, 1945b). The metathoracic tergum consists mainly of the *notum*, the *postnotum* being visible, as in the mesothorax, only dorsolaterally. Medially the notum is quite narrow and partially concealed by the mesoscutellum (Fig. 7), but laterally it becomes broader. Its anterior wall (the "presentum" of Tower, 1913) is continuous medially with the posterior wall of the second phragma. Laterally the notum is separated from the phragma by a narrow membrane (concealed, in Figures 7-9, by the scutellar process). Larsén (1942) has pointed out that this separation enables the lateral edges of the metanotum to be bent downwards, indirectly causing the extension and raising of the hindwing. The lateral border of the metanotum bears both an *anterior* and a *posterior notal wing process* (Fig. 8, *AWIII* and *PWIII*), although Larsén (1945b) reported the latter to be absent in the Heteroptera. In the wing membrane ventral to the posterior notal wing process and the *third axillary sclerite* (to be described later) lies an extremely minute *subalare* which is easily overlooked (Figs. 8 and 11, *SBIII*).

The medial part of the metanotum bears a broadly U-shaped groove (Fig. 7) which produces a ridge on the inner surface. This groove appears to turn laterally just before the posterior notal border and to run to a point just behind the posterior notal wing process (Fig. 8). It may represent a *scutoscutellar suture* (*SL*) ("V-Leiste" of Larsén, 1945a and b). If so, the narrow notal region behind it may be termed the *scutellum* (*SMIII*) and the more extensive area anterior to it the *scutum* (*SCIII*). The posterolateral part of the scutellum resembles the scutellar process of the mesothorax. The *axillary cord* of the hindwing (Fig. 8, *ACIII*) comes off from the lateral edge of this region, but the subalare is not joined to the scutellum as it is in the mesothorax.

The medial part of the narrow postnotum (*PNIII*) is concealed by the notum; laterally it becomes somewhat broader and is visible dorsally (Fig. 7) and laterally (Fig. 11). It joins the metathoracic epimeron to form the *postalar bridge* (Fig. 8, *POBIII*) just posterior to the axillary cord. The posterior margin of the postnotum continues into the anterior wall of the *third phragma;* the latter, which marks the dorsal boundary between the thorax and abdomen, is a low ridge without ventral processes (Fig. 12, *P3*). It is much less pronounced than the second phragma.

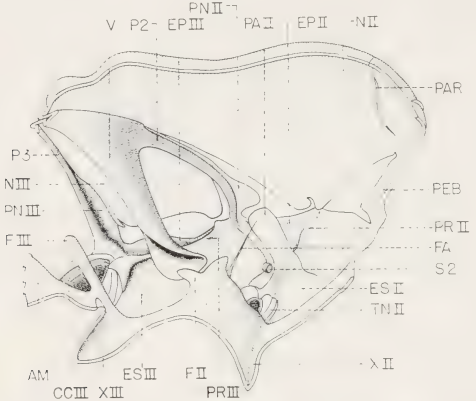


Figure 12. Medial view of the left half of the pterothorax, with the muscles removed. Only the bases of the coxae are shown.

PLEURON

Mesothorax. The intersegmental membrane (I) from the prothorax meets the pleuron of the mesothorax along the medial edge of the prealar bridge and the anterior margin of the mesothoracic *episternum* (Fig. 10). Within the membrane, just anterior to the most dorsal part of the prealar bridge, lies a very small sclerite (*SE*) which provides an insertion for one of the depressor muscles of the thorax. According to Larsén (1945b), this sclerite is a free lateral part of the first phragma.

A ventral view of the mesothorax (Fig. 13) shows an extensive episternum (*ESII*) and a somewhat smaller *epimeron* (*EPII*) separated by a long and distinct *pleural suture* (*PSII*). Both these sclerites have *supracoxal lobes* overlapping the coxal bases as in the prothorax; in addition, a *posterior lobe of the epimeron* (*ELII*), which is continuous with the epimeral supracoxal lobe, overlaps part of the metathoracic episternum, concealing the lateral boundary between the mesothoracic and metathoracic pleura (Fig. 14). At the posterolateral corner of this posterior epimeral lobe is a conspicuous knob (Figs. 7 and 14, *K*) ("Höcker" of Larsén, 1945a and b) which fits into a depression on the anterior margin of the forewing and thus holds the resting

Figure 13. Ventral view of the pterothorax. The legs, except for the right coxae, have been removed and the forewings have been cut off near their bases.

wing firmly in place. Dorsal and considerably anterior to this knob, the epimeron meets the mesopostnotum forming the postalar bridge (Fig. 11).

Ventral to the base of the wing, both pleural sclerites are somewhat evaginated to form a sort of shelf; in the epimeron, this shelf continues into the posterior epimeral lobe (Fig. 11). Dorsal to this evaginated portion, at the point where the epimeron joins the episternum, is a short *pleural wing process* ("wing fulcrum" of Taylor, 1918) (Figs. 8 and 11, *WPII*). This process lies ventral and lateral to the anterior notal wing process. The dorsal margin of the epimeron is somewhat thickened and curved

medially, which helps to strengthen and support the pleural wing process.

The *coxal cavity* is bordered medially by the sternum and laterally by the pleural sclerites (Fig. 15). Anterior to it lies a very broad *precoxal bridge* where the episternum is fused indistinguishably with the sternum. It is difficult to determine whether or not a *postcoxal bridge* is present, since the boundary between the mesosternum and metasternum is uncertain. According to Larsén (1945b), the boundary between these two regions is marked by the mesosternal furcae. If this criterion is used, the mesosternal-metasternal boundary must lie just at or slightly behind the posterior margin of the mesocoxal cavity. If the former is true, the postcoxal bridge is absent; if the latter, the bridge is very narrow, probably being represented by the slight ridge bordering the posterior edge of the coxal cavity (Fig. 15, *RG*). On this ridge, one of the metathoracic muscles, *M. episterno-coxalis* (Muscle 66), originates. Larsén (1945a) considered the point of origin of this muscle to be the anterior part of the metathoracic episternum, immediately behind the intersegmental boundary. If such is the case, the mesothoracic postcoxal bridge must be absent.

At the lateral margin of the coxal cavity there is a conspicuous *coxal process* (Fig. 15, *CPII*) from which the distinct *pleural ridge* (*PRII*) runs anterodorsally on the inner surface of the pleuron (Figs. 12 and 15). There is no basicoxal plate ("freie Basicoxalplatte" of Larsén, 1945d). The entire length of the pleural ridge is visible. About midway along the pleural ridge is a rectangular *pleural apophysis* (*PAII*) (possibly the "basalare apodeme" of Akbar, 1957), which bends somewhat posterolaterally and extends towards the second phragma.

Metathorax. The metathoracic pleuron is composed mostly of the *episternum* (Fig. 13, *ESIII*) with its large *supracoxal* and *posterior lobes*. These lobes, which are continuous with each other, overlap part of the abdomen. The greatly reduced *epimeron* possesses no supracoxal lobe, and is visible only laterally (Fig. 11, *EPIII*). Anteriorly the episternum is covered by the posterior lobe of the mesothoracic epimeron. This lobe covers both the intersegmental boundary between the mesopleura and metapleura and the *second thoracic spiracle* (Figs. 12, 14, and 15, *S2*)

which is located at the anterior edge of the metathoracic episternum. The posterior margin of the mesothoracic epimeral lobe lies very closely upon the metathoracic episternum, and it seems unlikely that air could reach the spiracle from a posterior direction. Laterally, however, between the posterior lobe of the mesothoracic epimeron and the metathoracic episternum, there is a space which bears some resemblance to the "air chamber" of corixids, as described by Griffith (1945). The air reaching the second thoracic spiracle probably comes in through this space, which is located directly beneath the base of the hindwing. This condition is typical of the aquatic Heteroptera rather than the terrestrial bugs, as Larsén (1945b) has pointed out.

The *coxal cavity* is very large and oval in shape, its long axis running mediolaterally in relation to the body (Fig. 15). Anteriorly it is bordered by a very broad *precoxal bridge* which joins the episternum with the sternum, and anteromedially by the metasternum. Posteriorly and posteromedially it is bordered by the abdominal sternites. There is no postcoxal bridge or basicoxal plate. A very large *coxal process* (*CPIII*) articulates laterally with the base of the *coxa*. This process has an anterior extension which articulates with the *trochantin* (*TNIII*) (to be described later). Dorsal to the coxal process a high *pleural ridge* (*PRIII*) extends anterolaterally for a short distance and then curves to run directly anteriorly, parallel to the longitudinal axis of the body (Fig. 15). Externally only the dorsal part of the *pleural suture* (*PSIII*), which ends in the *pleural wing process* (*WPIII*), is visible (Fig. 11); the ventral part of the suture is concealed by the lateral part of the metathoracic posterior episternal lobe. There is no pleural apophysis in the metathorax.

Across the precoxal bridge runs a deep *stink groove* (Fig. 14, *SG*) which produces a high *stink ridge* internally (Fig. 15, *SR*). The groove extends from the external orifice of the thoracic stink gland, at the base of the furca, to the point where the posterior mesothoracic epimeral lobe begins to overlap the metathoracic episternum. The part of the precoxal bridge, anterior to the groove corresponds to the "anterior laterale" plus the "basisternum" of Brindley (1934), the "basisternum" of Griffith (1945), and the "laterale" of Akbar (1957); the part posterior to the groove represents the "antecoxal laterale" of Brindley

(1934), the "episternum" of Griffith (1945), and the "antecoxal" of Akbar (1957). The anteromedial wall of the groove forms a narrow flap (Fig. 14, *AF*) (the "stink fold" of Akbar, 1957, and the "anterior laterale" of Brindley, 1934), which extends posteriorly, while the posterolateral wall forms an even larger flap (*PF*) in the lateral part of the groove. This second flap extends anteriorly and overlaps the smaller one. Together the two flaps form a partial covering over the ventral side of the groove, helping to hold the secretion in the channel. The form and position of the stink groove is more like that of the aquatic Heteroptera, as described by Larsén (1945b), than like that of

Figure 14. Ventral view of the posterior portion of the pterothorax, left side, showing the stink groove. The legs have been removed. The broken lines indicate the positions of the anterior metathoracic episternum and of the second thoracic spiracle, which are overlapped by the posterior lobe of the mesothoracic epimeron.

the terrestrial bugs; Larsén did not consider the stink grooves of these two groups to be homologous. There is an especially strong resemblance between the grooves of *Gelastocoris* and the Corixidae, the chief difference being that the corixids lack the larger of the two flaps.

Just beyond the lateral end of the stink groove, the posterior edge of the mesothoracic posterior epimeral lobe is modified to form a very smooth, shiny band (Fig. 14, *EV*), whose surface contrasts sharply with the rough texture of the rest of the sclerite. This band is so placed that the secretion emerging from the stink groove flows out upon it. It probably serves as an *evaporating*

surface for the secretion; to the author's knowledge, such an evaporating surface has not been reported in any other heteropteran.

The epimeron is largest in the anteroposterior direction. Posterodorsally it joins the postnotum to form the postalar bridge, and posterolaterally it is somewhat produced to form a posteriorly projecting lobe (the "epimeral flap" of Akbar, 1957) (Fig. 11). Just ventral to this lobe the epimeron is more or less fused with an anterolateral process from the abdomen (Figs. 11 and 15, *AP*). This process, the "Pleura des ersten Abdominalsegments" of Larsén (1945a) and the "epimeral fold" of Akbar (1957), bears the *first abdominal spiracle* at its base, and appears to be abdominal in nature; Snodgrass (1909) considered it to be part of the abdomen in *Benacus*.

STERNUM

Mesothorax. Like the prosternum, the mesosternum possesses an evaginated triangular *xiphus* between the coxae (Fig. 13, *XII*). Along the posteroventral edge of the xiphus runs a *xiphal ridge* (*XRII*) similar to that of the prothorax; internally it appears as a groove (Fig. 15, *XG*). Unlike the corresponding ridge of the prosternum, it does not reach the coxal cleft, but runs instead to the anteromedial border of the coxal cavity. Since it does not pass through the furcal bases, it probably does not represent a sternacostal suture.

Just medial to the coxal cavities lie the conspicuous, oval *furcal pits* (Figs. 13 and 14, *FPII*). They mark the broad bases of the large *furcae* (Figs. 12 and 15, *FII*). The latter possess anterior and posterior arms (together probably corresponding to the "posterior arm of the endosternite" of Rawat, 1939) which extend dorsally nearly to the ventral processes of the second phragma. From the more anterior furcal arm a long, slender *furcal apodeme* (*FA*) ("anterior arm of the endosternite" of Rawat, 1939; "Furcaapodem" of Larsén, 1945a and b; "anterior process of the furca" of Griffith, 1945; "lateral arm of the mesothoracic furca" of Lauck, 1959) extends dorsolaterally and nearly touches the tip of the pleural apophysis.

There is no clear boundary between the mesosternum and the metasternum. As has been previously mentioned, the mesosternal furcae probably indicate its approximate position.

Metathorax. The *xiphus* ("sternellum" of Griffith, 1945) of the metasternum is considerably larger than those of the preceding two segments (Fig. 13, *XIII*). Along its posteroventral margin runs a ridge (*SS*) which resembles the xiphal ridges of the prothorax and mesothorax. Since it ends at the bases of the metathoracic furcae, however, it may represent a *sternacostal suture.* If so, the part of the sternum anterior to it may be termed the *basisternum,* and the short portion posterior and lateral to it (the posterodorsal wall of the xiphus) may be

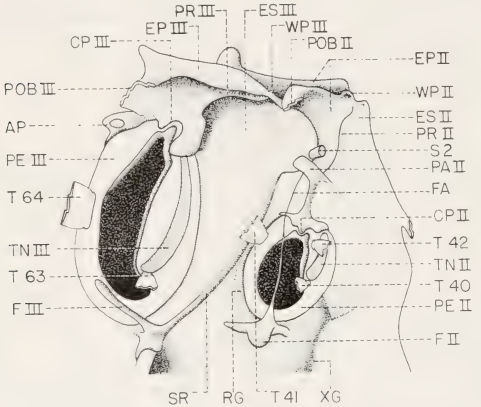


Figure 15. Dorsal view of the inner surface of the pterothorax, left side, showing the sterna and pleura. The pterotergum has been cut off at the postalar bridges and at the mesothoracic prealar bridge, and the tendons in the pericoxal membranes have been cut off near their bases. The muscles have been removed.

called the *sternellum* or *furcasternum.* Extending between the metathoracic furcae is a membrane which separates the metathoracic sternum from the sternum of the first abdominal segment.

The *furcal pits* are concealed externally by the lateral edges of the xiphus. Internally the furcae appear as two unbranched processes (Figs. 12 and 15, *FIII*). They extend posterolaterally and are longer and much more slender than the mesothoracic furcae.

Legs

The raptorial forelegs of *Gelastocoris* are oriented differently, with respect to the body, than are the walking and jumping pterothoracic legs. For convenience, however, the descriptive terms applied to the surfaces of the last two pairs of legs will be the same as those used for the corresponding surfaces of the forelegs. The terms "anterior" and "posterior" are here applied to the anteromedial and posterolateral sides of the foreleg respectively; "ventral" refers to the inner surfaces (those which

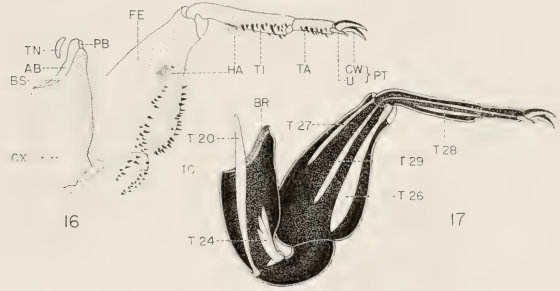


Figure 16. Medial view of the left prothoracic leg and trochantin.

Figure 17. Medial view of the inner surface of the left prothoracic leg, showing the tendons.

meet, on the femur and tibia, when the latter are apposed), and "dorsal" refers to the outer surfaces. The numbers used to designate the various tendons are the same as those of the muscles which insert on them.

Prothoracic legs (Figs. 6, 16, and 17). The prothoracic coxal cavity is fairly round. In the anterior part of the *pericoxal membrane* (*PE*) ("coxal corium" of Griffith, 1945, and Akbar, 1957) lies a small *trochantin* (*TN*), which does not appear to articulate with either the pleuron or the base of the *coxa*. The coxa is therefore articulated only at the coxal process, and this single joint allows it to move freely in all directions. Such freedom of movement is advantageous in a raptorial leg; Rawat

(1939) has reported a similar condition in the foreleg of *Naucoris*. Four tendons in the pericoxal membrane provide insertions for the muscles which move the coxa; *Tendon 13* is located just medial to the medial end of the trochantin, to which it is partially attached, *Tendon 14* just lateral to the lateral end of the trochantin, *Tendon 15* slightly posterior to the coxal process, and *Tendon 16* in the posteromedial region of the pericoxal membrane.

The coxa (*CX*) is nearly cylindrical in form, and projects out farther from the body than do the coxae of the second and third pairs of legs. A *basicostal suture* (*BS*) encircles its proximal end; posteromedially the suture is very faint and close to the edge, but laterally it becomes clearer, producing a *basicostal ridge* (*BR*) ("basicosta" of Snodgrass, 1935) internally. It separates off an *anterior basicoxite* (*AB*) ("vorderes Basicoxale" of Larsén, 1945c) anterior to the coxal process, and an equally large *posterior basicoxite* (*PB*) ("hinteres Basicoxale" of Larsén, 1945c) posterior to that process. Snodgrass (1935) termed the posterior basicoxite the "meron"; Larsén (1945c and d), however, has shown that the posterior basicoxite and the meron are two separate elements, and that the latter is absent in the Heteroptera. Between the two basicoxites the basal coxal rim is invaginated to form a socket (the "articular process" of Griffith, 1945) into which the coxal process fits.

A dicondylic joint with anterior and posterior articulations joins the coxa with a short, curved *trochanter* (*TC*). On the ventral surface of the latter are two irregular rows of short spines. Two tendons, whose bases are attached to the proximal rim of the trochanter by tough membranes, extend into the coxa. The longer of these, *Tendon 20,* is located in the part of the rim which is farthest from the femur, and reaches into the thoracic cavity. A shorter, three-branched *Tendon 24* comes from the part of the rim nearest the femur.

A dicondylic joint with dorsal and ventral articulations joins the trochanter with the *femur* (*FE*). These two segments are joined so closely together that the condyles are difficult to see. The femur is greatly thickened to accommodate the powerful tibial muscles which originate on its inner walls. These muscles enable the *tibia* (*TI*) to open and close upon the femur. The femur is broadest proximally, the dorsal part of the segment

forming a hump above the articulation with the trochanter. The ventral surface of the femur is flattened, and an irregular row of stout spines extends along each side of the flattened area. On the anterior surface of the femur, just dorsal to the row of spines, is a comb of long, fine hairs (*HA*). This meets a similar comb of hairs on the tibia when the two segments are brought together. It probably serves, as Weber (1930) has suggested, as a cleaning organ for the head and antennae; the insects often perform "grooming" movements with their forelegs in the region of the head.

The femur and tibia are joined by a dicondylic joint with anterior and posterior articulations. The ventral surface of the tibia is flattened, and bears two rows of spines similar to those of the femur. When the tibia and femur are closed upon each other, prey may be caught between the apposed flattened areas and held in place by the spines. Two long tendons from the ventral (*Tendon 26*) and dorsal (*Tendon 27*) regions of the proximal edge of the tibia extend into the femur. The base of Tendon 26 is expanded into a broad sclerotized plate (the "genuflexor plate" of Akbar, 1957) which is movably bound to the rim of the tibia.

The tibia and *tarsus* (*TA*) are joined primarily by a membrane, but have a weak anterior and posterior dicondylic joint. From the ventral region of the proximal edge of the tarsus, *Tendon 28* extends into the tibia. There is only one tarsal segment. Distally the tarsus is joined by a membrane to the *pretarsus* (*PT*), which consists of two fairly long, stout *claws* (*CW*) and a ventral plate, the *unguitractor* (*U*) ("flexor plate" of Rawat, 1939). The distal end of the unguitractor is narrowed, and bears two very fine, short spines. Akbar (1957) reported similar spines in *Leptocorisa* and suggested that they may be analagous with the "empodium" of Diptera. From the base of the unguitractor, a very long *Tendon 29* ("depressor apodeme" of Akbar, 1957) extends through the tarsus and tibia and into the femur.

Mesothoracic legs (Figs. 15 and 18). Unlike the first pair of legs, the second and third pairs have coxae which articulate with the pleuron at two points. Their movement is thus more restricted. A small invagination of the lateral rim of the *mesocoxa*

forms a socket into which the coxal process fits; in addition, a rather broad *trochantin* (*TNII*) articulates medially with the anterior margin of the coxa and laterally with an anterior extension of the coxal process. Three tendons in the *pericoxal membrane* (*PEII*) provide insertions for muscles; *Tendon 40* lies just beside the medial end of the trochantin and is partially attached to the latter, *Tendon 41* is located in the posterior region of the pericoxal membrane, and *Tendon 42* lies just anterior and medial to the coxal process.

Figure 18. Medial view of the left mesothoracic leg and trochantin.

Figure 19. Medial view of the left metathoracic leg and trochantin.

The mesothoracic coxae lie closer to the body than do those of the prothorax. They project posteromedially, nearly touching each other at the midline (Fig. 2). Distally they are nearly spherical in shape; proximally the side which contacts the coxal process is considerably longer than the opposite side. The *basicostal suture* is not as marked as that of the prothorax. It seems to disappear medially, while laterally it separates off the very narrow *anterior* and *posterior basicoxites*.

The joints between the various segments of the leg are essentially the same as those of the prothoracic leg. Also the tendons within the segments occupy the same positions as those of the

first pair of legs, their terminology and the corresponding prothoracic tendons being as follows: *Tendon 46* (Tendon 20), *Tendon 50* (Tendon 24), *Tendon 52* (Tendon 26), *Tendon 53* (Tendon 27), *Tendon 54* (Tendon 28), *Tendon 55* (Tendon 29).

The mesothoracic *femur* is longer and not nearly as broad as that of the prothorax, and it lacks the flattened ventral area. The *tibia* is also longer, and the *tarsus* consists of two segments, the first one being much reduced. The *unguitractor* of the *pretarsus* resembles that of the forelegs, and possesses similar terminal spines; the pretarsal *claws* are smaller than those of the first pair of legs. On the ventral surfaces of the *trochanter* and femur are rows of short spines. The tibia possesses longer spines on all its surfaces; these are especially numerous distally. A few spines are also present on the distal segment of the tarsus.

Metathoracic legs (Figs. 15 and 19). The metathoracic *coxae*, like those of the preceding segment, project posteromedially; distally they are very spherical, while proximally the side which contacts the coxal process is much elongated. They are articulated with the pleuron both directly, at the coxal process, and indirectly, by means of the very long *trochantin* (*TNIII*). Unlike the coxae of the two anterior pairs of legs, the metathoracic coxa forms a narrow lateral process at its rim, this process fitting into a socket on the coxal process; in the prothorax and mesothorax, the socket is on the coxa. The *pericoxal membrane* (*PEIII*) possesses only two tendons: *Tendon 63*, which is partially attached to the medial end of the trochantin, and *Tendon 64*, in the posterior part of the membrane. At the proximal end of the coxa, the *basicostal suture* separates off a distinct *posterior basicoxite* and a very narrow *anterior basicoxite*.

The form of the various joints and tendons is the same as in the first pair of legs. The terminology of the different tendons is as follows: *Tendon 70* (Tendon 20), *Tendon 74* (Tendon 24), *Tendon 76* (Tendon 26), *Tendon 77* (Tendon 27), *Tendon 78* (Tendon 28), and *Tendon 79* (Tendon 29).

The shapes of the *femur*, *tibia* and *tarsus* are quite different from those of the corresponding segments of the forelegs. Since the latter are modified for catching prey, while the former are adapted for jumping, these differences are not surprising. The

metathoracic femur is much longer and narrower than the prothoracic one. In the Hemiptera, according to Weber (1930), the main muscles of the jumping legs are those of the *trochanter*, not those of the tibia as in Orthoptera. In the gelastocorid foreleg, on the other hand, the tibial muscles are greatly developed for capturing prey, and therefore the femora, on which these muscles originate, are much enlarged. The metathoracic tibia and tarsus are also much longer than those of the foreleg, and the tarsus is three-segmented, the proximal segment being reduced. The great length of the femur, tibia, and tarsus provides additional leverage for jumping.

On the femur there are a few very fine spines or hairs, but very stout spines are present only on the tibia and tarsus, where they are very numerous. In addition, the ventral surfaces of the tibia and tarsus bear rows of long, fine hairs; there are two such rows on the tibia and one on the tarsus. Weber (1930) has suggested that the spines on the last two pairs of legs in gelastocorids help to anchor the legs in the sand and to prevent them from slipping backwards when the animal is jumping. The metathoracic tibial and tarsal hairs are probably used to clean the sides of the abdomen; the author has often observed live gelastocorids rubbing their hindlegs over the edges of the abdomen.

Wings

Forewing. Most of the forewing is coriaceous, and its surface is covered with tubercles of various sizes, similar to those on the body. Its tip, the *membrane* (*MB*), is smooth-textured and less coriaceous. The rest of the wing is divided into *clavus* (*CV*), *corium* (*CO*), and *embolium* (*EM*), as shown in Figure 20. The boundaries between these areas are marked by very narrow membranous clefts in the surface of the wing. These probably represent wing veins, but the author will not attempt to homologize them. Both Tanaka (1926) and Hoke (1926) studied the veins of the forewings of a few Heteroptera, but none of the species studied by them resembles *Gelastocoris* closely enough to permit comparison. The boundary between the clavus and the corium is very clear, and the wing possesses a flexible fold along this line. The embolium is marked off by a long longitudinal and a short

transverse vein; these two do not meet medially. A fourth vein runs longitudinally along the middle of the clavus; it is difficult to see in many specimens.

The anterolateral edge of the embolium is greatly thickened and folded ventrally. In this thickened, folded region there is a large, socket-like depression which receives the knob on the posterolateral margin of the mesothoracic epimeron, holding the resting wing securely in place. Similar wing-locking devices have been reported in a great many Heteroptera by many authors,

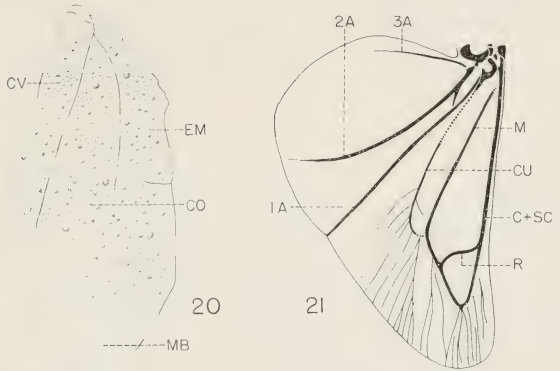


Figure 20. Dorsal view of the right forewing.

Figure 21. Dorsal view of the right hindwing.

and appear to be a common feature in this order of insects. As has been previously mentioned, the pleural sclerites ventral to the base of the forewing are somewhat evaginated, forming a shelf-like projection. The thickened edge of the embolium lies upon this shelf when the wing is at rest.

The axillary sclerites by which the forewing articulates with the mesothorax are shown in Figure 9. The *first axillary sclerite* (*1AX*), which articulates with the anterior notal wing process, is small and oval in shape; laterally it contacts a large, irregularly shaped *second axillary sclerite* (*2AX*). The latter is fused

anteriorly with the *humeral plate* (*H*), the boundary between the two being indistinct. A U-shaped *third axillary sclerite* (*3AX*) articulates anterolaterally with the posterior part of the second sclerite; posteromedially it is movably joined with a small *fourth axillary sclerite* (*4AX*). A suture divides this fourth sclerite into a proximal and a distal part, the proximal part articulating medially with the subalare. Lateral to the anterolateral portion of the third axillary sclerite is a small, triangular *median plate* (*MP*). This sclerite articulates anteriorly with a larger process (*MP?*) which appears to be the lateral part of the second axillary sclerite, but which may represent a second median plate which has become fused with that sclerite. A similar situation is found in the forewings of the belostomatids *Benacus* and *Lethocerus;* both Snodgrass (1909) and Lauck (1959), who studied those forms, considered the process in question to be a median plate.

Hindwing. Figure 21 shows the veins of the hindwing of *Gelastocoris.* For convenience, the homologies suggested by Hoke (1926) are used here. That author, who studied the wing venation of representatives of 25 families of Heteroptera, figured the hindwing of *Gelastocoris* sp.

As shown in Figure 9, the *first axillary sclerite* (*1AX*) of the hindwing articulates with the anterior notal wing process of the metathorax and is very small. The *third axillary sclerite* (*3AX*) is much larger and articulates with the posterior notal wing process; Taylor (1918) mistook it, in *Belostoma*, for the subalare. The third axillary sclerite is broad and U-shaped, bearing a small, knob-like projection laterally. This projection contacts the base of the *second anal vein* (Fig. 21, *2A*). Between the first and third sclerites lies a small *second axillary sclerite* (*2AX*); an even smaller, triangular *median plate* (*MP*) is located just lateral to the second axillary sclerite.

MUSCULATURE

In general, the names of the following muscles and the numbers by which they are designated are the same as those used by Larsén (1945a). A few of the muscles described by Larsén appear to consist of two parts in *Gelastocoris;* in such cases they

have been given the name proposed by that author, with the addition of "primus" or "secundus", and an "A" or "B" has been added to Larsén's number. All the thoracic muscles are paired.

An attempt has been made to list, for each muscle, similar muscles which have been reported in other Heteroptera. Those listed are included because both their origins and their insertions, as described in the literature, are the same or very similar to those of the corresponding muscle in *Gelastocoris*. Whether or not they are actually homologous to the gelastocorid muscle which they resemble cannot, in most cases, be definitely stated. The names used by Larsén are given only when they differ from those employed in the current work.

In Figures 22-31, the muscles are designated by the numbers given below.

Muscles of the prothorax

1. M. PRONOTI PRIMUS (Fig. 22)

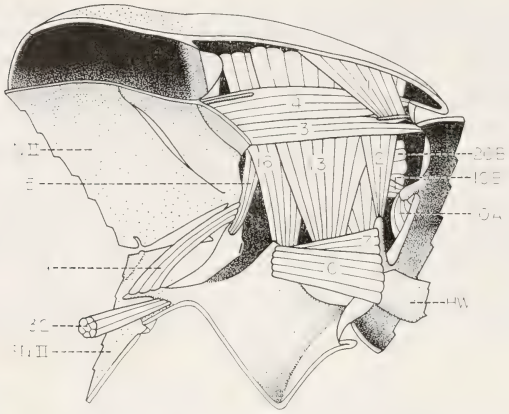
   Origin: Anteromedial region of the pronotum.
   Insertion: On the two tendons in the mid-dorsal region of the cervical membrane.
   Action: Raises and retracts the head.

2. M. PRONOTI SECUNDUS (Fig. 22)

   Origin: Anterior region of the pronotum, lateral to *M. pronoti primus.*
   Insertion: Tip of the occipital condyle.
   Action: Rotates or depresses the head.
   Similar muscles: Muscle 1 and Muscle 2 (?) (Malouf, 1933); cephalic depressor (?) (Rawat, 1939); first and second pairs of levators of head (Akbar, 1957).

3. M. PRONOTI TERTIUS (Fig. 22)

   A well developed longitudinal muscle.
   Origin: Ventral part of the first phragma.
   Insertion: On the dorsomedial margin of the postocciput, and on the two tendons in the cervical membrane.
   Action: Rasies and retracts the head.
   Similar muscles: Tergal longitudinal muscle (Malouf, 1933); ventral fibers of dorsal muscle (Rawat, 1939); indirect levators of head (Akbar, 1957).



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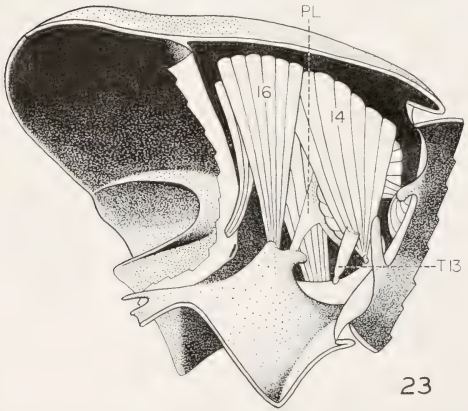

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Figure 22. Medial view of the left half of the prothorax showing the more medial muscles. The left halves of the postocciput and of the anterior part of the mesothorax are shown in place.

Figure 23. Same view as above. The mesothorax and Muscles 1, 2, 3, 4, 6, 7, 9, and 13 have been removed. Tendon 13 has been cut off near its base.

4. M. PRONOTI QUARTUS (Fig. 22)
   A well developed longitudinal muscle, just dorsal to *M. pronoti tertius*.
   Origin: On the dorsal part of the first phragma, and on the two tendons in the intersegmental membrane.
   Insertion: On the inturned dorsomedial margin of the pronotum.
   Action: Raises the prothorax.
   Similar muscles: Muscle rétracteur du prothorax (Poisson, 1924); dorsal fibers of dorsal muscle (Rawat, 1939).

5. M. PRONOTI QUINTUS (Fig. 22)
   A slender muscle.
   Origin: On the small sclerite in the intersegmental membrane anterior to the prealar bridge of the mesothorax.
   Insertion: Posterior region of the pronotum.
   Action: Depresses the prothorax.
   Similar Muscles: Indirect protractor of fore legs (Malouf, 1933); depressors of pronotum (?) (Akbar, 1957).

6. M. PROSTERNI PRIMUS (Fig. 22)
   A broad longitudinal muscle.
   Origin: Anterior surface of the medial arm of the prothoracic furca.
   Insertion: On the occipital condyle and on the tip of the hypopharyngeal wing.
   Action: Depresses and retracts the head. May also cause some rotation.
   Similar muscles: Sternal longitudinal muscle (Malouf, 1933); depresso-extensors of head (Akbar, 1957).

7. M. PROSTERNI SECUNDUS (Fig. 22)
   A broad longitudinal muscle, just lateral to *M. prosterni primus*.
   Origin: Anterior surface of the lateral arm of the prothoracic furca.
   Insertion: Occipital condyle.
   Action: Same as *M. prosterni primus*.

9. M. DORSOVENTRALIS (Fig. 22)
   A slender muscle.
   Origin: Anterior margin of the prealar bridge of the mesothorax, medial to *M. pronoti quintus*.
   Insertion: Posterior sternal process of the prothorax.
   Action: Raises the posterior part of the prosternum, thus depressing the prothorax as a whole.
   Similar muscles: Tergo-sternal furcal muscle (Rawat, 1939); fu_1-$prsc_2$ (Lauck, 1959).

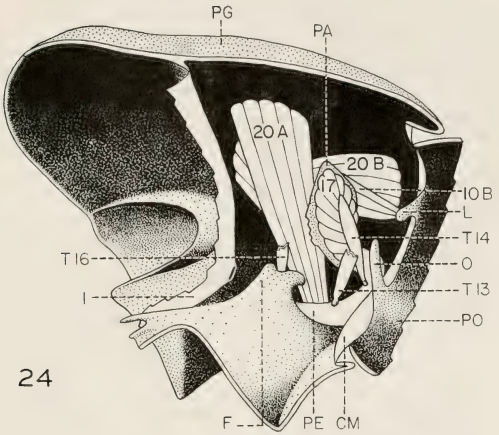
10A. M. PROEPISTERNO-POSTOCCIPITALIS PRIMUS (Fig. 22)
A short muscle.
Origin: Anterolateral region of the proepisternum.
Insertion: Lateral apodeme of the postocciput.
Action: Raises the head (contraction of both muscles) or moves it to one side (contraction of one muscle).
Similar muscles: Part of M. proepisterno-postoccipitalis (Larsén, 1945a); promoto-extensors of head (?) (Akbar, 1957).

10B. M. PROEPISTERNO-POSTOCCIPITALIS SECUNDUS (Figs. 22 and 24)
A short muscle.
Origin: Lateral surface of the prothoracic pleural apophysis.
Insertion: Tip of the lateral apodeme of the postocciput.
Action: Depresses the head (contraction of both muscles) or moves it to one side (contraction of one muscle).
Similar muscle: Part of M. proepisterno-postoccipitalis (Larsén, 1945a).

13. M. NOTO-TROCHANTINALIS (Fig. 22)
A large, fan-shaped muscle.
Origin: Pronotum, just lateral to *M. pronoti primus.*
Insertion: Tendon 13, at the medial end of the trochantin.
Action: Rotates the coxa and promotes the leg.
Similar muscles: Tergal promotor of coxa (?) (Malouf, 1933); tergal promotor (Rawat, 1939); first promotor of coxa (?) (Akbar, 1957).

14. M. NOTO-COXALIS PRIMUS (Fig. 23)
A large, fan-shaped muscle.
Origin: Pronotum, lateral to *M. pronoti secundus* and *M. noto-trochantinalis.*
Insertion: Tendon 14, lateral to the trochantin.
Action: Rotates the coxa and abducts the leg.
Similar muscles: Internal rotator (Rawat, 1939); second promotor of coxa (?) (Akbar, 1957).

15. M. NOTO-COXALIS SECUNDUS (Fig. 25)
A large, fan-shaped muscle.
Origin: Posterolateral region of the pronotum.
Insertion: Tendon 15, just posterior to the coxal process.
Action: Rotates the coxa and remotes the leg.
Similar muscles: External rotator (Rawat, 1939); first remotor of coxa (?) (Akbar, 1957).



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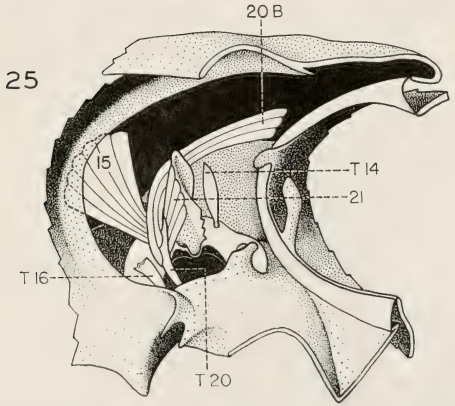

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Figure 24. Same view as Fig. 22. Muscles 5, 10A, 14, and 16 have been removed. Tendon 16 has been cut off near its base, and the pleurosternal bridge has been cut away.

Figure 25. Posteromedial view of the left half of the prothorax and of the postocciput (same view as Fig. 5), showing Muscles 15, 20B, and 21. The posterior lobes of the pronotum and epimeron have been cut away, and the pleurosternal bridge has been removed.

16. M. NOTO-COXALIS TERTIUS (Figs. 22 and 23)
A large, fan-shaped muscle.
Origin: Pronotum, posterior and lateral to *M. noto-trochantinalis.*
Insertion: Tendon 16, in the posteromedial region of the pericoxal membrane.
Action: Rotates the coxa and adducts the leg.
Similar muscles: Tergal remotor of coxa (?) (Malouf, 1933); tergal remotor (Rawat, 1939).

17. M. PLEURA-COXALIS (Fig. 24)
A short, broad muscle.
Origin: Medial surface of the prothoracic pleural apophysis.
Insertion: Tendon 14.
Action: Same as *M. noto-coxalis primus.*

20A. M. NOTO-TROCHANTERALIS PRIMUS (Fig. 24)
A long, well-developed muscle.
Origin: Pronotum, between *M. noto-coxalis secundus* and *M. noto-coxalis tertius.*
Insertion: Tendon 20, from the part of the proximal rim of the trochanter which is farthest from the femur.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, tergal branch (Malouf, 1933); extra-coxal depressor, branch from tergum (Rawat, 1939); part of M. noto-trochanteralis (Larsén, 1945a); tergal depressor of trochanter (Akbar, 1957).

20B. M. NOTO-TROCHANTERALIS SECUNDUS (Figs. 22, 24, and 25)
A long, slender muscle.
Origin: Anterolateral region of the pronotum, very near the lateral margin of the episternum.
Insertion: Tendon 20.
Action: Depresses the trochanter.
Similar muscles: Extra-coxal depressor, branch from tergum (?) (Rawat, 1939); part of M. noto-trochanteralis (Larsén, 1945a).

21. M. PLEURA-TROCHANTERALIS (Fig. 25)
A short, broad muscle.
Origin: Lateral surface of the prothoracic apophysis.
Insertion: Tendon 20.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, pleural branch (Malouf, 1933); extra-coxal depressor, branch from pleural region (Rawat, 1939); pleural depressor of trochanter (?) (Akbar, 1957).

Muscles of the mesothorax

30. M. MESONOTI PRIMUS (Fig. 26)

When developed, this is the largest muscle in the thorax. In the majority of specimens, however, it, like the other indirect flight muscles, is degenerate.

Origin: Anterior surfaces of the medial part of the second phragma and of the ventral processes of the latter.

Insertion: First phragma and prescutum of the mesothorax.

Action: Indirect flight muscle. Depresses the forewing by acting in antagonism to *M. dorsoventralis primus* and *M. mesonoti secundus*.

Similar muscles: Muscle vibrateur dorsal longitudinal (Poisson, 1924); tergal longitudinal muscle (Malouf, 1933); dorsal muscles of mesothorax (Rawat, 1939); indirect and principal depressor of fore-wings (Akbar, 1957); 1ph-2ph and sc_2-2ph (Lauck, 1959).

31. M. MESONOTI SECUNDUS (Figs. 26 and 27)

Quite large when developed; degenerate in the majority of specimens.

Origin: Lateral surface of the ventral process of the second phragma.

Insertion: Anterolateral region of the mesoscutum.

Action: Indirect flight muscle, raising the forewings. Its contraction forces the anterior notal wing process downward upon the first axillary sclerite. Since the pleural wing process forms a fulcrum upon which the second axillary sclerite pivots, the rest of the wing is forced upwards.

Similar muscles: Tergal longitudinal oblique muscle (Malouf, 1933); secondary indirect levator of fore-wings (Akbar, 1957); sc-scl_2-2ph (Lauck, 1959).

32. M. MESOSTERNI PRIMUS (Figs. 22 and 26)

A fairly long, well-developed muscle.

Origin: Anterior surface of the mesothoracic furca.

Insertion: Posterior part of the prosternum, between the posterior sternal processes.

Action: Depresses the prothorax.

Similar muscles: Sternal longitudinal muscle (?) (Malouf, 1933); ventral muscle of mesothorax (Rawat, 1939); fu_1-fu_2 (Lauck, 1959).

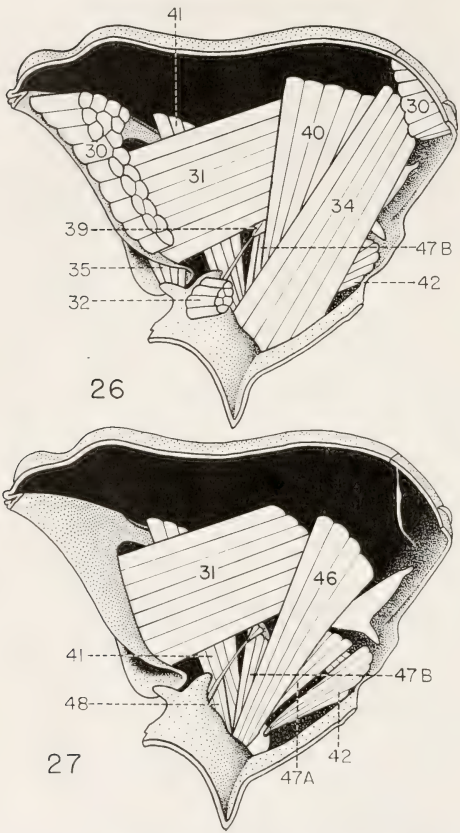

Figure 26. Medial view of the left half of the mesothorax (same view as Fig. 12 *f*, showing the more medial mesothoracic muscles. The middle part of Muscle 30 has been cut away. Muscles 30, 31, and 34 are fully developed in this specimen.

Figure 27. Same view as above. Muscles 30, 32, 34, 35, and 40 have been removed. Tendon 40 is not shown.

34. M. DORSOVENTRALIS PRIMUS (Fig. 26)

Large when developed; degenerate in the majority of specimens.

Origin: In a depression on the mesothoracic precoxal bridge, just anterior to the coxal cavity.

Insertion: Anterior part of the mesoscutum, just lateral to the parapsidal ridge.

Action: Same as *M. mesonoti secundus.*

Similar muscles: Muscle vibrateur transversal (sternali-dorsal) (Poisson, 1924); tergo-sternal muscle (Malouf, 1933); indirect and principal levator of fore-wings (Akbar, 1957); sc_2-bs_2 (Lauck, 1959).

35. M. DORSOVENTRALIS SECUNDUS (Fig. 26)

A very short muscle.

Origin: Posterior arm of the mesothoracic furca.

Insertion: Tip of the ventral process of the second phragma, between the two layers of this process.

Action: Depresses the posterior mesotergum and the anterior metatergum (?).

Similar muscles: Tergo-sterno-furcal muscle (Malouf, 1933); tergo-sternal furcal muscle of mesothorax (Rawat, 1939); secondary indirect depressor of fore-wings (Akbar, 1957); 2ph-fu_2 (Lauck, 1959).

38. M. EPISTERNO-ALARIS (Fig. 30)

Lies beneath *M. pleura-trochanteralis primus* and *M. episterno-coxalis.*

Origin: Anterior region of the mesothoracic episternum, just posterior to the point of origin of *M. episterno-coxalis.*

Insertion: On a tendon from the "elbow" of the third axillary sclerite of the forewing.

Action: Direct flight muscle. Contraction causes the third axillary sclerite to flip over, thus flexing a previously extended forewing.

Similar muscles: First flexor of fore wing (Malouf, 1933; Akbar, 1957); axillary muscle of mesothorax (Rawat, 1939); 3ax_2-eps_2 (Lauck, 1959).

39. M. FURCA-PLEURALIS (Figs. 26 and 30)

A very minute muscle.

Origin: Tip of the mesothoracic furcal apodeme.

Insertion: Tip of the mesothoracic pleural apophysis.

Action: Uncertain.

Similar muscles: Sterno-pleuro-apophysal muscle (Malouf, 1933); pleurosternal muscle (Rawat, 1939); promoto-extensor of fore-wings (?) (Akbar, 1957); plr_2-fu_2 (Lauck, 1959).

40. M. NOTO-TROCHANTINALIS (Fig. 26)

A well-developed, fan-shaped muscle.

Origin: Mesoscutum, between *M. dorsoventralis primus* and *M. noto-trochanteralis.*

Insertion: Tendon 40, at the medial end of the mesothoracic trochantin.

Action: Rotates the coxa and promotes the leg.

Similar muscles: Tergal promotor of coxa (Malouf, 1933); tergal promotor of mesothorax (Rawat, 1939); sc-scl$_2$-cx$_2$ (Lauck, 1959).

41. M. NOTO-COXALIS (Figs. 26, 27, and 30)

A well-developed, fan-shaped muscle.

Origin: Posterolateral limit of the mesoscutum.

Insertion: Tendon 41, in the posterior region of the pericoxal membrane.

Action: Rotates the coxa and remotes the leg.

Similar muscles: Tergal remotor of coxa (Malouf, 1933); tergal remotor of mesothorax (Rawat, 1939); first remotor of coxa (Akbar, 1957); sc-scl$_2$'-cx$_2$' (Lauck, 1959).

42. M. EPISTERNO-COXALIS (Figs. 26, 27, and 30)

A rather small, fan-shaped muscle.

Origin: Anterior part of the mesothoracic episternum, in the region of the prealar bridge.

Insertion: Tendon 42, just anterior to the coxal process.

Action: Rotates the coxa and promotes the leg.

Similar muscles: Sternal promotor of coxa (?) (Malouf, 1933); second promotor of coxa (Akbar, 1957); eps$_2$-cx$_2$ (Lauck, 1959).

46. M. NOTO-TROCHANTERALIS (Fig. 27)

A well-developed muscle.

Origin: Mesoscutum, between *M. mesonoti secundus* and *M. noto-trochantinalis.*

Insertion: Tendon 46, from the part of the proximal rim of the trochanter which is farthest from the femur.

Action: Depresses the trochanter.

Similar muscles: Depressor of telopodite, tergal branch (Malouf, 1933); extra-coxal depressor of the trochanter of the mesothorax, tergal branch (Rawat, 1939); tergal depressor of trochanter (Akbar, 1957); sc-scl$_2$-tr$_2$ (Lauck, 1959).

47A. M. PLEURA-TROCHANTERALIS PRIMUS (Figs. 27 and 30)
A rather slender muscle.
Origin: Anterior part of the mesothoracic episternum, just lateral to *M. episterno-coxalis.*
Insertion: Tendon 46.
Action: Depresses the trochanter.
Similar muscles: Depressor of telopodite, pleural branch (Malouf, 1933); extra-coxal depressor of the trochanter of the mesothorax, pleural branch (Rawat, 1939); part of M. pleura-trochanteralis (Larsén, 1945a); pleural depressor of trochanter (Akbar, 1957); eps_2-tr_2 (Lauck, 1959).

47B. M. PLEURA-TROCHANTERALIS SECUNDUS (Figs. 26, 27, and 30)
Origin: Medial surface of the mesothoracic pleural apophysis.
Insertion: Tendon 46.
Action: Depresses the trochanter.
Similar muscles: Extra-coxal depressor of the trochanter of the mesothorax, pleural branch (Rawat, 1939); part of M. pleura-trochanteralis (Larsén, 1945a).

48. M. FURCA-TROCHANTERALIS (Figs. 27 and 30)
A small muscle, rather difficult to see.
Origin: Base of the furcal apodeme of the mesothorax.
Insertion: Tendon 46.
Action: Depresses the trochanter.
Similar muscles: Extra-coxal depressor of the trochanter of the mesothorax, sternal branch (Rawat, 1939); fu_2-tr_2 (Lauck, 1959).

Muscles of the metathorax

60. M. DORSOVENTRALIS (Fig. 28)
A slender muscle.
Origin: Tip of the metathoracic furca.
Insertion: Third phragma, lateral to the midline.
Action: Depresses the posterior part of the metanotum (?).
Similar muscles: Tergo-sternal furcal muscle of metathorax (Rawat, 1939); 3ph-fu_3 (Lauck, 1959).

61. M. EPISTERNO-ALARIS (Figs. 29 and 30)
A very slender muscle, difficult to see.
Origin: Lateral part of the metathoracic episternum, just lateral to the point of origin of *M. pleura-trochanteralis.*
Insertion: On a tendon from the "elbow" of the third axillary sclerite of the hindwing.

Action: Direct flight muscle. Flexes the hindwing in the same way that *M. episterno-alaris* of the mesothorax flexes the forewing.

Similar muscles: Flexor of hind wing (Malouf, 1933); axillary muscle of metathorax (Rawat, 1939); first flexor of hindwings (Akbar, 1957); 3ax-eps$_3$ (Lauck, 1959).

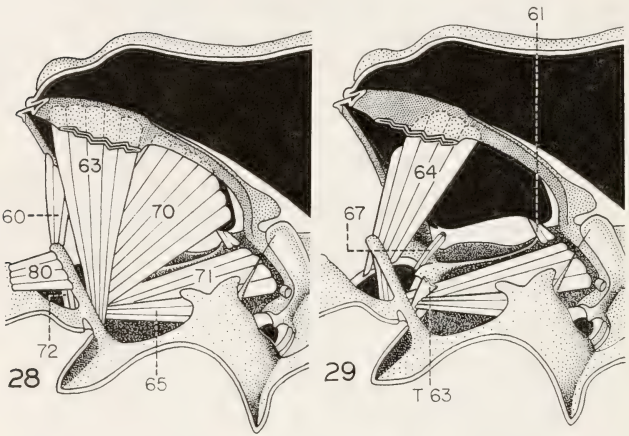

Figure 28. Medial view of the left halves of the metathorax and of the posterior mesothorax (same view as Fig. 12), showing the more medial metathoracic and abdominal muscles. The ventral process of the second phragma has been cut off.

Figure 29. Same view as above. Muscles 60, 63, 70, and 80 have been removed.

63. M. NOTO-TROCHANTINALIS (Fig. 28)

A well-developed, fan-shaped muscle.

Origin: Anterior part of the metanotum, just lateral to the midline.

Insertion: Tendon 63, at the medial end of the metathoracic trochantin.

Action: Rotates the coxa and promotes the leg.

Similar muscles: Tergal promotor of coxa (Malouf, 1933); tergal promotor of metathorax (Rawat, 1939); first promotor of coxa (?) (Akbar, 1957); sc$_3$-ex$_3$ (Lauck, 1959).

64. M. NOTO-COXALIS (Figs. 29 and 30).

A well-developed, fan-shaped muscle.

Origin: Metanotum, lateral and posterior to *M. noto-trochantinalis.*

Insertion: Tendon 64, in the posterior part of the pericoxal membrane.

Action: Rotates the coxa and remotes the leg.

Similar muscles: Tergal remotor of coxa, first branch (Malouf, 1933); tergal remotor of metathorax (Rawat, 1939); first remotor of coxa (Akbar, 1957); sc_3'-ex_3' (Lauck, 1959).

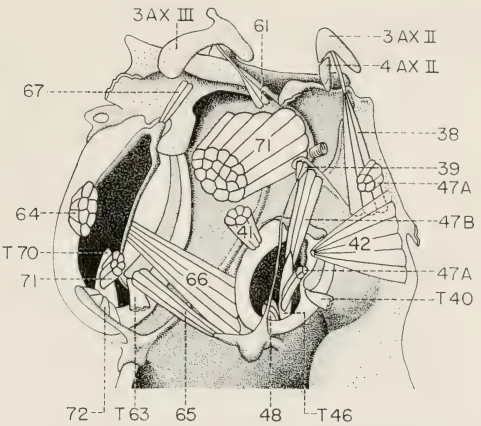

Figure 30. Dorsal view of the inner ventral surface of the pterothorax, left side (same view as Fig. 15), showing the ventral and lateral muscles. The middle parts of Muscles 47A and 71 have been cut away, and most of the tendons of the leg muscles, along with Muscles 41 and 64, have been cut off near their bases. The third and fourth axillary sclerites are shown in place.

65. M. FURCA-TROCHANTINALIS (Figs. 28 and 30)

A slender muscle, rather difficult to see.

Origin: Base of the posterior arm of the mesothoracic furca.

Insertion: On Tendon 63 and on the medial end of the metathoracic trochantin.

Action: Rotates the coxa and promotes the leg.

Similar muscle: M. episterno-trochantinalis (?) (Larsén, 1945a).

66. M. EPISTERNO-COXALIS (Fig. 30)
A flat, broad muscle lateral to *M. furca-trochantinalis.*
Origin: On the ridge bordering the posterior margin of the mesothoracic coxal cavity (Larsén, 1945a, considered this ridge to be part of the metathoracic episternum).
Insertion: Anterior margin of the anterior basicoxite of the metathoracic coxa.
Action: Rotates the coxa and promotes the leg.
Similar muscle: Sternal promotor of metathorax (?) (Rawat, 1939).

67. M. COXA-SUBALARIS (Figs. 29 and 30)
A slender muscle.
Origin: On the basicostal suture of the metathoracic coxa, in the region of the coxal process.
Insertion: On the very small metathoracic subalare.
Action: Direct flight muscle. Depresses the posterior margin of the hindwing.
Similar muscles: Depressor of posterior margin of hind wing (Malouf, 1933); second flexor of hind-wings (Akbar, 1957).

70. M. NOTO-TROCHANTERALIS (Fig. 28)
A very well-developed muscle.
Origin: Lateral part of the metanotum.
Insertion: Tendon 70, from the part of the proximal rim of the trochanter which is farthest from the femur.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, tergal branch (Malouf, 1933); extra-coxal depressor of the trochanter of the metathorax, tergal branch (Rawat, 1939); tergal depressor of trochanter (Akbar, 1957); sca-tra (Lauck, 1959).

71. M. PLEURA-TROCHANTERALIS (Figs. 28 and 30)
A very well-developed muscle.
Origin: Lateral and anterolateral region of the metathoracic episternum.
Insertion: Tendon 70.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, pleural branch (Malouf, 1933); extra-coxal depressor of the trochanter of the metathorax, pleural branch (Rawat, 1939); pleural depressor of trochanter, (Akbar, 1957).

72. M. FURCA-TROCHANTERALIS (Figs. 28 and 30)
Origin: Base of the metathoracic furca.
Insertion: Tendon 70.

Action: Depresses the trochanter.
Similar muscles: Extra-coxal depressor of the trochanter of the metathorax, sternal branch (Rawat, 1939); fu3-tr3 (Lauck, 1959).

80. M. VENTRALIS ABDOMINALIS (Fig. 28)
A short, broad abdominal muscle.
Origin: Posterior surface of the metathoracic furca.
Insertion: On a ridge on the ventrolateral part of the second abdominal segment.
Action: Raises the abdomen.
Similar muscles: veM1 (Larsén, 1945a); fu3-2S (Lauck, 1959).

INTRINSIC MUSCLES OF THE LEGS
Prothoracic legs (Fig. 31)

23. M. COXA-TROCHANTERALIS MEDIALIS
A short, broad, well-developed muscle.
Origin: Posteromedial wall of the coxa.
Insertion: Tendon 20.
Action: Depresses the trochanter.
Similar muscles: Coxal branch of depressor of trochanter (Malouf, 1933); depressor of the trochanter (Rawat, 1939); coxal depressor of trochanter (Akbar, 1957).

24. M. COXA-TROCHANTERALIS LATERALIS
A muscle consisting of three bundles.
Origin: Anterior wall of the coxa.
Insertion: On the three-branched Tendon 24, from the part of the proximal rim of the trochanter which is nearest the femur.
Action: Raises the trochanter.
Similar muscles: Levator of trochanter (as shown in Pl. XVI, fig. 1, by Malouf, 1933; Rawat, 1939; Akbar, 1957).

25. M. REDUCTOR FEMORIS
A short, broad muscle.
Origin: Posteromedial wall of the trochanter.
Insertion: Lateral part of the proximal margin of the femur. Some strands enter the femur and insert on Tendon 26.
Action: Moves femur laterally. Strands entering the femur depress the tibia.
Similar muscles: Remotor of femur (Malouf, 1933); reductor of the femur (Rawat, 1939; Akbar, 1957).

26. M. DEPRESSOR TIBIAE

A very well-developed muscle.

Origin: Walls of the ventral half of the femur.

Insertion: Tendon 26, from the ventral region of the proximal margin of the tibia.

Action: Depresses the tibia, closing it upon the femur.

Similar muscles: Depressor of tibia (Malouf, 1933; Rawat, 1939; Akbar, 1957).

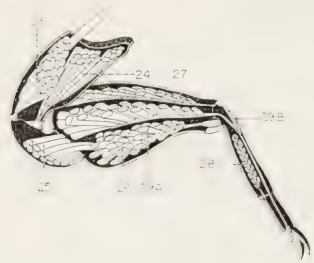

Figure 31. Medial view of the left prothoracic leg, with the medial walls of the leg removed (same view as Fig. 17), showing the intrinsic leg muscles.

27. M. LEVATOR TIBIAE

Less well-developed than *M. depressor tibiae*.

Origin: Walls of the most dorsal part of the femur.

Insertion: Tendon 27, from the dorsal region of the proximal margin of the tibia.

Action: Raises the tibia.

Similar muscles: Levator of tibia (Malouf, 1933; Rawat, 1957); extensor of tibia (Akbar, 1957).

28. M. DEPRESSOR TARSI

Composed of many short, fine muscle strands.

Origin: Ventrolateral walls of the tibia.

Insertion: Tendon 28, from the ventral region of the proximal margin of the tarsus.

Action: Depresses the tarsus.

Similar muscles: Depressor of tarsus (Malouf, 1933; Rawat, 1939; Akbar, 1957).

29A. M. DEPRESSOR PRAETARSI PRIMUS

A well-developed muscle.

Origin: Lateral walls of the dorsal half of the femur, between *M. depressor tibiae* and *M. levator tibiae.*

Insertion: Intrafemoral part of Tendon 29, from the unguitractor of the pretarsus.

Action: Depresses the pretarsus.

Similar muscles: Depressor of pretarsus, femoral branch (Malouf, 1933; Rawat, 1939); part of M. depressor praetarsi (Larsén, 1945a); depressor of pretarsus, proximal muscle (Akbar, 1957).

29B. M. DEPRESSOR PRAETARSI SECUNDUS

A very weak muscle, consisting of only a few strands.

Origin: Proximal region of the dorsal wall of the tibia.

Insertion: Intratibial part of Tendon 29.

Action: Depresses the pretarsus.

Similar muscles: Depressor of pretarsus, tibial branch (Malouf, 1933; Rawat, 1939); part of M. depressor praetarsi (Larsén, 1945a); depressor of pretarsus, distal muscle (Akbar, 1957).

Pterothoracic legs

Each of the following muscles (Nos. 49-55B and Nos. 73-79B) corresponds to a similar muscle in the foreleg which bears the same name. The origins, insertions, and actions of the corresponding muscles are similar, and each muscle, with the exception of *M. coxa-trochanteralis medialis,* inserts on a tendon bearing the same number as the muscle. In the following account, for each pterothoracic muscle the number of the corresponding prothoracic muscle will be noted, along with any significant differences in general appearance.

Mesothoracic legs

49. M. COXA-TROCHANTERALIS MEDIALIS
Similar to Muscle 23. Inserts on Tendon 46.

50. M. COXA-TROCHANTERALIS LATERALIS
Similar to Muscle 24.

51. M. REDUCTOR FEMORIS
Similar to Muscle 25.

52. M. DEPRESSOR TIBIAE
Similar to Muscle 26, but less well developed.

53. M. LEVATOR TIBIAE
Similar to Muscle 27, but somewhat less well developed.

54. M. DEPRESSOR TARSI
Similar to Muscle 28.

55A. M. DEPRESSOR PRAETARSI PRIMUS
Similar to Muscle 29A, but much less well developed.

55B. M. DEPRESSOR PRAETARSI SECUNDUS
Similar to Muscle 29B.

Metathoracic legs

73. M. COXA-TROCHANTERALIS MEDIALIS
Similar to Muscle 23. Inserts on Tendon 70.

74. M. COXA-TROCHANTERALIS LATERALIS
Similar to Muscle 24.

75. M. REDUCTOR FEMORIS
Similar to Muscle 25.

76. M. DEPRESSOR TIBIAE
Similar to Muscle 26, but much less well developed.

77. M. LEVATOR TIBIAE
Similar to Muscle 27, but less well developed.

78. M. DEPRESSOR TARSI
Similar to Muscle 28; the muscle strands are shorter and weaker.

79A. M. DEPRESSOR PRAETARSI PRIMUS
Similar to Muscle 29A, but much less well developed.

79B. M. DEPRESSOR PRAETARSI SECUNDUS
Similar to Muscle 29B.

DISCUSSION

Among the Heteroptera, degeneration of the flight muscles, such as has been observed in the large majority of the gelastocorids examined, is not uncommon. Many species have individuals which are unable to fly because of reduction of the wings, of the muscles, or of both. Polymorphism of the wings is found in some terrestrial families, such as the Pyrrhocoridae, Aradidae, and Lygaeidae (Weber, 1930) and in many aquatic and semi-aquatic families. Poisson (1924), who studied polymorphism in the aquatic Corixidae, Aphelocheiridae, and Naucoridae, and in the semi-aquatic Gerridae, Hydrometridae, Veliidae, and Mesoveliidae, found that individuals with reduced wings usually showed degenerate flight muscles, although in a few cases the muscles were normal. Larsén (1950) found that in *Aphelocheirus* the degree

of reduction of the flight musculature increased in proportion to the amount of reduction of the wings.

Degeneration of the flight muscles in normal-winged individuals, as in *Gelastocoris*, is also quite common in both aquatic and terrestrial Heteroptera (Larsén, 1950). Among the aquatic forms, it has been reported in the Nepidae, Naucoridae, and Aphelocheiridae (Ferrière, 1914; Poisson, 1924; Larsén, 1949 and 1950). In their general appearance, the degenerate muscles of *Gelastocoris* closely resemble the reduced muscles of macropterous individuals of *Aphelocheirus*, as illustrated by Larsén (1950; his Fig. 8b). The degenerate dorsal longitudinal muscles of the mesothorax were termed the "tracheo-parenchymatous organ" by some authors because of the abundance of tracheoles which penetrate them. Early workers such as Dufour (1833) and Dogs (1909) believed this "organ" to be respiratory in function. It appears, however, that the tracheoles are only those which would penetrate a normal muscle, and that the tracheo-parenchymatous organ has no special respiratory function (Ferrière, 1914; Brocher, 1916). A degenerate *M. mesonoti primus* of *Gelastocoris*, when teased apart and examined under a compound microscope, shows a rich supply of tracheoles similar to those figured by Ferrière in the tracheo-parenchymatous organ of *Nepa*.

One puzzling feature noted in the present investigation is that although some gelastocorids possess well developed flight muscles as well as normal wings none of the insects were ever observed to fly. During nearly a year of captivity they were constantly given opportunities to do so, but never showed any inclination towards flight. Larsén (1950) made a similar observation on a few individuals of *Ranatra* which never flew even when strongly stimulated to do so. Examination of their musculature showed it to be normal. That author proposed that this might be due to a reduction of the nervous component of the flight apparatus. Whether or not this is a plausible explanation for the lack of flight in *Gelastocoris* may be elucidated by further anatomical work. Todd (1955), who also observed no flight in *Gelastocoris oculatus*, has noted that several other species of Gelastocoridae have forewings which are fused or which have reduced membranes, and in some species the hindwings are reduced.

The present study offers a few clues to the possible phylogenetic position of the Gelastocoridae among the Heteroptera. A brief review of the literature on this problem has been presented in a previous paper (Parsons, 1959), and the reader is referred to that work for a discussion of the theories of earlier authors. It is generally agreed that the three littoral families Gelastocoridae, Ochteridae, and Saldidae are closely related to each other, the first-named family having arisen from the second. It also appears that these three families represent a stage in the evolution of the totally aquatic and semi-aquatic bugs (the Hydrocorisae and Amphibicorisae respectively) from the terrestrial forms (the Geocorisae). Authorities have disagreed, however, as to which of the littoral families are related to the Hydrocorisae and which to the Amphibicorisae. De la Torre-Bueno (1923) believed the Hydrocorisae to be descended from saldid-like ancestors, with the ochterids and gelastocorids as intermediate stages. Spooner's (1938) work on the head capsule led him to place the latter two families with the Amphibicorisae, and the saldids with the Geocorisae. More recently, China (1955) has proposed that the Amphibicorisae arose from "Proto-Saldidae" and the Hydrocorisae from "Proto-Ochteridae."

Larsén (1945b), after studying a large number of heteropteran families, found five characteristics of the thoracic skeleton which seem to be more typical of the Hydrocorisae than of the other Heteroptera. First, the metanotum of the aquatic bugs is longer than the metapostnotum; in the Geocorisae the latter is longer than the former, while in *Salda* (Saldidae) the two are equal in length. Unfortunately, the boundary between these two regions is indistinct in the Amphibicorisae studied by Larsén, so that it is difficult to compare them with the Hydrocorisae and Geocorisae. The present study has shown the metanotum of *Gelastocoris* to be much longer than the metapostnotum, and in this character it resembles the Hydrocorisae.

A second feature of the Hydrocorisae, according to Larsén, is the presence, in all three thoracic segments, of a distinct pleural ridge (except in the mesothorax of *Ranatra*). Taylor (1918) also pointed out the distinctness of the pleural ridge in the pterothorax of corixids, belostomatids, and notonectids. In all the semi-aquatic and terrestrial bugs studied by Larsén, the pleural

ridge is indistinct in at least one segment. A distinct prothoracic pleural ridge with a pleural apophysis is present in all of the Hydrocorisae studied by Larsén, but in only three of the Geocorisae and in none of the Amphibicorisae. In *Gelastocoris*, however, all three segments show distinct pleural ridges, and a prothoracic pleural apophysis is present. A large posterior lobe on the mesothoracic epimeron is a third character distinguishing the Hydrocorisae. This lobe is quite extensive in *Gelastocoris*, overlapping much of the metathoracic episternum, and its size is comparable to that of the aquatic bugs *Hesperocorixa*, *Notonecta*, and *Pelocoris*. In the Amphibicorisae, in *Salda*, and in most of the Geocorisae studied by Larsén the posterior mesothoracic epimeral lobe is more weakly developed. Two other Geocorisae showing weakly developed mesothoracic epimeral lobes are *Nezara* (Malouf, 1933) and *Leptocorisa* (Akbar, 1957).

A fourth characteristic of the aquatic bugs, as cited by Larsén, concerns the width of the metathoracic epimeron which is not as reduced as in many terrestrial bugs. Unfortunately, he did not compare the width of this sclerite in the Amphibicorisae and the Hydrocorisae, and did not state how many, if any, Geocorisae are exceptions to this generalization. The metathoracic epimeron of *Gelastocoris* appears to be as well developed as that of the aquatic bugs *Hesperocorixa*, *Notonecta*, *Pelocoris*, *Belostoma*, *Nepa*, and *Ranatra*. Finally, Larsén stated that the mesothoracic pleural apophysis in the Hydrocorisae is large and extends dorsally. The size of this process in *Gelastocoris* is comparable to that of *Belostoma* and of *Naucoris* as figured by Larsén (1945a); it appears to be somewhat smaller than that of *Notonecta*, but is considerably larger than that of *Hesperocorixa* and *Ranatra*. It extends dorsally, like the pleural apophyses of the aquatic forms. Among the semi-aquatic bugs, according to Larsén (1945a and b), the mesothoracic pleural apophysis is absent in *Velia*, small in *Gerris*, and well developed in *Hydrometra*; among the Geocorisae it is variable in both size and position (Larsén, 1945b). Malouf's (1933) figure of the mesothoracic pleural apophysis in the terrestrial bug *Nezara* shows it to be fairly small and medially directed.

In a few other features of the thoracic skeleton, *Gelastocoris* resembles the Hydrocorisae, Amphibicorisae, or Geocorisae.

Larsén (1945b) found a distinct separation between the metathoracic scutum and scutellum only in the aquatic and semi-aquatic bugs. Although Akbar (1957) described a clear separation between these two regions in the metanotum of *Leptocorisa,* a terrestrial bug, it seems that his interpretation is open to criticism; the part termed the "scutum" by him seems to be the notum, while his "scutellum" (as shown in his Fig. 66) resembles the postnotum. Malouf (1933) also incorrectly described a distinct metascutum and metascutellum in *Nezara,* as Larsén (1945b) has pointed out. On the gelastocorid metanotum there is a fairly definite groove which may represent a scutoscutellar suture; if this interpretation is correct, this character links the gelastocorids with both the Hydrocorisae and the Amphibicorisae.

Larsén (1945b) also reported the prothoracic postcoxal bridge to be broader than the precoxal bridge in the majority of Hydrocorisae; this is also the case in *Gelastocoris.* In the Geocorisae and Amphibicorisae, either the precoxal bridge is the broader of the two or both bridges are equal in size. This does not serve to distinguish the Hydrocorisae as a whole, however, since in *Notonecta* and *Corixa,* according to Larsén, the postcoxal bridge is narrower than the precoxal.

Larsén (1945b) found that although the metathoracic subalare is present in most terrestrial bugs it is absent in most aquatic (with the exception of *Notonecta*) and semi-aquatic forms. The presence of a metathoracic subalare in *Gelastocoris* is, therefore, a character most commonly found in the Geocorisae; this sclerite is, however, much reduced in *Gelastocoris.*

The thoracic musculature does not shed as much light on the phylogenetic problem as does the thoracic skeleton. Larsén's comparative study revealed very few differences between the three major heteropteran groups on the basis of musculature. Three generalizations can be made, however. First, the two dorsal longitudinal muscles of the heteropteran metathorax ("Mm. metanoti primus" and "secundus" of Larsén, 1945a) are absent in all the Hydrocorisae examined by that author, while at least one of the two is present in *Salda,* in all the Amphibicorisae, and in all but two of the Geocorisae. *Gelastocoris* resembles the aquatic bugs in this respect, since it lacks both metathoracic dorsal longitudinal muscles. Secondly, the ventral longitudinal

muscle of the abdomen (*M. ventralis abdominalis* of the present study) is well developed in all Larsén's Hydrocorisae and in *Salda,* but is weak or absent in most of the semi-aquatic and terrestrial forms examined by him. Here again, *Gelastocoris* resembles the Hydrocorisae. Thirdly, a *M. coxa-subalaris* is present in both the mesothorax and the metathorax of most of the terrestrial bugs studied by Larsén, but is absent in the aquatic and semi-aquatic forms, the only exception being its presence in the metathorax of *Notonecta.* The presence of this muscle in the metathorax of *Gelastocoris* links this bug with the Geocorisae; the link is not very strong, however, since *Notonecta* also possesses this muscle in the metathorax, and since the muscle is absent in the mesothorax of *Gelastocoris.*

In general, therefore, the skeleton and musculature of the thorax of *Gelastocoris* bear more resemblance to those of the Hydrocorisae than to those of the Amphibicorisae or Geocorisae. This is in agreement with the conclusions reached in a previous study of the gelastocorid head (Parsons, 1959), and supports the phylogenetic theory of China (1955). Similarities to the aquatic bugs are seen in the structure of the metatergal sclerites, the presence of distinct pleural ridges in all three segments, the size of the mesothoracic and metathoracic epimera, the degree of development of the mesothoracic pleural apophyses, and the breadth of the prothoracic posteoxal bridge. Further resemblances to the aquatic Heteroptera are the absence of metathoracic dorsal longitudinal muscles and the presence of *M. ventralis abdominalis.* The gelastocorids also resemble both the Hydrocorisae and the Amphibicorisae in the separation between the metascutum and the metascutellum. Only two features of the gelastocorid thorax are atypical of the Hydrocorisae; in their possession of a metathoracic subalare and subalar muscle, they resemble the Geocorisae (although these two characters are also found in *Notonecta,* which is definitely one of the Hydrocorisae). It must be borne in mind, however, that there are exceptions in the literature to all of the above generalizations, and that these are not clear-cut distinctions.

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EXPLANATION OF FIGURES

In the figures, the membranes, the muscles, the tendons, and the cut edges of the skeleton are unstippled, while the skeletal surfaces are either stippled or blackened. The muscles are indicated by the numbers given in pages 329-346. Each major tendon is indicated by a "T" followed by the number of the muscle attaching to it; when more than one muscle attaches to a tendon, the tendon's number is that of the lowest-numbered muscle. The numeral II after an abbreviation indicates a mesothoracic structure, while the numeral III indicates a metathoracic structure.

The abbreviations used in the figures are as follows:

1, 2, or 3 A — first, second or third anal vein
AB — anterior basicoxite
AC — axillary cord
AF — anteromedial flap of stink groove
AM — abdomen
AP — anterolateral abdominal process
AW — anterior notal wing process
1, 2 3, or 4 AX — first, second, third or fourth axillary sclerite
BR — basicostal ridge
BS — basicostal suture
C+CS — costa plus subcosta
CC — coxal cavity
CL — coxal cleft
CM — cervical membrane
CO — corium
CP — coxal process
CU — cubitus
CV — clavus
CW — claw
CX — coxa
EL — posterior epimeral lobe
EM — embolium
EP — epimeron
EPS — supracoxal lobe of epimeron
ES — episternum
ESS — supracoxal lobe of episternum
EV — evaporating surface
F — furca
FA — furcal apodeme
FE — femur

FP — furcal pit
FW — forewing
H — humeral plate
HA — comb of hairs on foreleg
HW — hypopharyngeal wing
I — intersegmental membrane
K — knob, on mesothoracic epimeron, for anchoring forewing
L — lateral apodeme
LP — posterior lobe of protergum
M — media
MB — membrane
MP — median plate
N — notum
O — occipital condyle
P 1, 2 or 3 — first, second, or third phragma
PA — pleural apophysis
PAR — parapsidal ridge
PAS — parapsidal suture
PB — posterior basicoxite
PC — precosta
PE — pericoxal membrane
PEB — prealar bridge
PEC — precoxal bridge
PF — posterolateral flap of stink groove
PG — protergum
PL — pleurosternal bridge
PM — prealar membrane
PN — postnotum
PO — postocciput
POB — postalar bridge
POC — postcoxal bridge
PR — pleural ridge
PS — pleural suture
PSP — posterior sternal process
PT — pretarsus
PU — prescutum
PW — posterior notal wing process
R — radius
RG — ridge bordering posterior edge of mesocoxal cavity
S 1 or 2 — first or second thoracic spiracle
SA — abdominal tympanal organ
SB — subalare
SC — scutum

SE — selerite for attachment of *M. pronoti quintus*
SG — stink groove
SL — scutoscutellar suture
SM — scutellum
SN — sternum
SP — scutellar process
SR — stink ridge
SS — sternacostal suture
ST — strut between posterior tergal and epimeral lobes of prothorax
T — tendon
TA — tarsus
TC — trochanter
TF — tergal fissure
TI — tibia
TN — trochantin
TR — transverse ridge
U — unguitractor
V — ventral process of second phragma
WG — wing groove
WP — pleural wing process
X — xiphus
XG — xiphal groove
XR — xiphal ridge

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THE PALATINE PROCESS OF THE PREMAXILLA IN THE PASSERES

A study of the variation, function, evolution and taxonomic value of a single character throughout an avian order

By Walter J. Bock
Biological Laboratories, Harvard University

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INTRODUCTION

Ever since the beginnings of avian taxonomy, ornithologists have concentrated on the species problem, with the study skin as the traditional object of study. This was in many ways a fortunate choice, and as a result, avian systematics on the species level is today the most advanced area in the field of taxonomy. But at the same time, interest in the higher categories of birds has lagged so far behind that we know virtually nothing about the affinities of most groups of birds. Even now, most systematic work on the supergeneric level represents scarcely more than guesswork, there is little agreement on the limits of the orders or on their relationships, and within the relatively sharply defined orders, the arrangements of the families are, at best, obscure. Most neglected of all the orders are the Passeres which, although they contain about half of the recent species of birds, have received less attention than any other group. The lack of interest in the anatomy as well as in the classification of the perching birds dates back to the beginnings of ornithology and is reflected in the attitude of the standard texts (Fürbringer, 1888; Gadow,

1891-93; and Beddard, 1898). These authors give detailed coverage of the families and even subfamilies of the non-passerine birds, yet they barely distinguish between the suborders of the perching birds, the tacit assumption being that their highly uniform morphology precludes the use of comparative anatomy as a basis for their classification. Unfortunately, this high degree of morphological similarity has usually been interpreted as uniformity, with the conclusion that comparative anatomical studies are of no use whatsoever in untangling the relationships within the Passeres.

Recently, there has been a revival of interest in the Passeres, as is indicated by the publication of a number of papers on their anatomy (Arvey, 1951; Ashley, 1941; Beecher, 1951a, 1951b, 1953; Berger, 1957; Engels, 1940; Fiedler, 1951; Hudson and Lanzillotti, 1955; Mayr, Andrew and Hinde, 1956; Moller, 1930, 1931; Nelson, 1954; Sims, 1955; Stalleup, 1954; Stonor, 1937, 1938, 1942; Sushkin, 1924, 1925, 1927, 1929; Swinebroad, 1954; and Tordoff, 1954a, 1954b). These papers have shown that the passerines are not absolutely uniform in their internal anatomy and that comparative anatomical studies may aid in the understanding of relationships on the familial level. With the removal of this psychological block and with increasing interest in the problems of passerine anatomy we may at last be on the way to understanding the evolution and classification of the perching birds.

This revival of interest in the Passeres is, however, not without its problems, of which the most important is the disagreement in interpretation of the morphological findings and their value in showing relationships. Stresemann (1959) has presented an excellent picture of the problems confronting avian systematics which should be read by every worker interested in this field. Mayr (1955, 1958) has discussed some of the perplexing evolutionary assumptions pertinent to passerine classification, and Starck (1959) has commented on some of the anatomical problems. These authors agree, more or less, that the major problems stem from the characters used as clues to relationships, and from uncritical use of the pertinent evolutionary and morphological principles. But something else is involved. Perhaps the difficulty arises from the relatively small degree of anatomical difference between passerine families; perhaps it stems from insufficient study of the characters or perhaps it is a result of the method by which the groups and their structures are compared. Undoubtedly, the answer is a combination of all three suggestions, but the

last one is probably the most important, and attention will therefore be focused on it.

The best approach in taxonomic studies is a comparison of as many characters as possible throughout the entire group. This ideal method is feasible only with comparatively small orders and families of birds. It is not practical when dealing with a large group such as the Passeres; alternate methods must be employed. These are of two types. The first is a comparison of as many characters as possible in two or more families. This is the method used in most of the works cited above. The second is an analysis of a single character or character-complex throughout the whole group under consideration. No proper study of this type has, to my knowledge, been made for the passerines. Therefore, this paper presents a sample study of a single character — the palatine process of the premaxilla — in the Passeres, as a basis on which some of the problems of passerine anatomy and classification may be explored.

The method of "single character study" is the analysis of all aspects of the character essential to understanding its evolution — this being the major goal of these studies. Although certain specialized aspects must be investigated in some cases, as for example, the embryology of the palatine process in this study, the following steps must be included in every "single character study."

a) A survey of the occurrence, structure and variation of the character must be undertaken. In general, the scope of the survey includes the next higher taxonomic category that contains the group under consideration. For instance, if the affinities of a passerine family are being studied, then the character must be surveyed throughout the Passeres. The degree of variation should be ascertained in each taxonomic group down to the species. All aspects of variation, e.g., sexual, age, geographical, must be separated and clearly distinguished from one another. Usually in studies of avian anatomy, it is not necessary to consider infrageneric variation, since most anatomical characters do not vary among congeneric species. This is especially true in the Passeres.

b) The functional significance of the character, including the meaning of its structural changes within the group, must be established. This is the most important part of the analysis of a taxonomic character and the one most often omitted or, if included, covered only in a superficial way. Because of limitations and technical difficulties, conclusions concerning the functions

are usually only deductions based on physical considerations of the morphology exhibited by the character. It is only rarely possible to observe the bird alive and to deduct the function from actual observations, or to conduct the necessary experiments to prove it conclusively. However, although most of these conclusions are only inferences, they are better than nothing and, with practice, a worker can infer the function of a structure with considerable accuracy. Two things must be remembered. First, such results are usually only rough approximations; we cannot hope, at this time, to determine the exact meaning of every minor variation in anatomical features. Second, as deductions, they are subject to error and hence the resulting conclusions regarding evolution and taxonomy are no better than the deductions on which they are based.

c) Lastly, the evolution of the character must be investigated. With a knowledge of its functional significance, one can estimate the selection forces which were operative during the evolution of the character. A knowledge of the selection forces is essential because while it is possible to outline the phylogeny of a structure without knowing the selection forces, it is impossible to understand its evolution without them. And here the important thing is the evolution, not the actual phylogeny, of the structure.

Once these aspects of a character are ascertained, it is possible to judge its taxonomic value. In general, the taxonomic value varies inversely with (a) the tightness of the control by the selection forces acting on the character, and (b) the changeability — independent origin, reversal of direction, etc. — of these selection forces. For example, if a structure is tightly bound to its selection forces, and if these selection forces have altered their direction frequently during the evolution of the group, then that structure would have little taxonomic value. Statements such as "the taxonomic value of a character depends upon how constant that character is within the group" are misleading and inconclusive. Lastly, I would like to suggest that the importance placed on the taxonomic value of a character be de-emphasized and that more stress be placed on studying its evolution. The former has not produced any really concrete results while the latter holds much promise for future studies of avian classification.

Before proceeding to the main part of the study, a word must be said about the classification and linear sequence of the passerine birds. The past lack of interest in the anatomy of the perching birds has resulted in chaos. In recent years, a number of conflicting classifications for the passerine families have been

proposed (Mayr and Amadon, 1951; Wetmore, 1951; Mayr and Greenway, 1956; Wetmore, 1957; Amadon, 1957; Delacour and Vaurie, 1957; and Mayr, 1958), yet these proposals and suggestions represent little more than personal opinion — the necessary information to verify the relationships suggested in these proposals does not exist. The central problem of passerine classification is the lack of factual evidence with which we can determine the evolution of the Passeres and eventually establish the most reasonable classification for them. Speculation on these problems is premature at the present time and it seems probable that it will be many years before enough information on the anatomy, behavior and other attributes of the passerines has been gathered to allow us to speculate on their phylogeny and relationships. Until that time comes, it is most advantageous to have a standard sequence of families which everyone knows and can use. For the purposes of this paper, I shall adopt the sequence agreed upon by the committee appointed by the XIth International Ornithological Congress at Basel which is the one to be used in the coming volumes of "Peters' Check-list" (Mayr and Greenway, 1956). This sequence covers only the Oscines. For the suboscines, I shall follow the sequence suggested by Wetmore (1951). I must emphasize that I do not believe that these particular systems are correct or even satisfactory. Nor do my findings support them better than the others. Nevertheless, it is strongly urged that workers in passerine anatomy follow the "Peters" sequence until enough evidence has been gathered to establish a classification acceptable to most workers.

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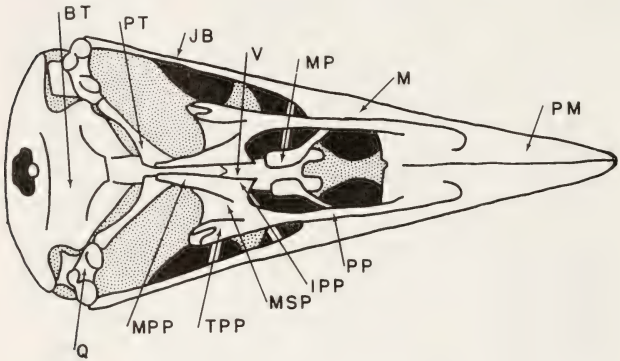

Figure 1. Ventral surface of the skull of a crow (*Corvus*). Note the absence of the palatine process of the premaxilla (= fused to the prepalatine process of the palatine). The deep-lying bones are stippled for contrast. The key for the abbreviations used in all figures can be found on pages 487-488.

DESCRIPTION OF THE PALATINE PROCESS OF THE PREMAXILLA

The palatine process is a posterior extension of the premaxilla starting from the medioventral part of that bone. It lies along the lateral edge of the palatine and fuses to a greater or lesser degree with that bone. The palatine process has many features that render it suitable for this study. It is a simple structure which is easily observable and which exhibits several quite dissimilar conditions in the Passeres. However, almost any other

anatomical feature that is not uniform throughout the order would be equally suitable for a study of this type.

It may occur in any one of four conditions — fused, unfused, free, or lateral flange.

Fused palatine process. In a typical passerine bird, such as a crow (*Corvus*, Fig. 1), we find the simplest possible adult condition of the palatine process of the premaxilla — namely, that it is lacking as a distinct structure. The anterior bars of the palatine (prepalatines or prepalatine processes) merge into the premaxillary mass without the slightest indication of a break. There are no sutures or processes at the junction of the prepalatine process and the premaxilla to reveal the presence of a palatine process of the premaxilla. The palatine process has fused completely with the prepalatine process, as will be shown later in the section on development. On the lateral side of the skull, the premaxilla merges with the maxilla, which in turn continues into the jugal bar.[1] The maxillo-palatines (not to be confused with the "palato-maxillaries") originate from the maxillae and pass medially beneath the palatines to approach one another in the region of the anterior end of the vomer. The distal ends of the maxillo-palatines expand to form flat plates; these plates partly cover the tip of the vomer when the ventral aspect of the palate is examined. Returning to the palatines, these bones run posteriorly and then expand medially to approach the midline. The palatine shelf[2] and the posterior extension of the palatines (the transpalatine process) serve as the point of origin for a large part of the M. pterygoideus (at least for the lateral parts of this muscle). The medial parts of the palatine (the interpalatine process, anteriorly, and the mediopalatine process, posteriorly),

[1] In his recent paper on the development of the chick skull, Jollie (1957) suggests that the names for a number of bones in the skull be changed to agree with their embryological origins and homologues in the reptilian skull. Thus, for example, the palatine would become the pterygopalatine and the pterygoid would become the posteropterygoid. These new names are certainly correct technically, but the change to them would not lead to greater clarity. The technically correct names are only necessary for comparisons of the avian skull with the skull of other classes of vertebrates; however, only a very few workers are interested in this problem. The terminology used currently for the parts of the avian skull was developed specifically for the adult skull, and in many cases the term refers to a functional region or unit rather than to an individual bone. The present system of names is perfectly suitable for studies in which the skull is compared within birds. Consequently, it is recommended that the standard terminology for the parts of the avian skull be retained. I do not, however, want to convey the impression that the embryological origin of the bones of the skull is unimportant. These studies are very important and indeed, many more studies similar to Jollie's investigation of the chick skull are needed.

[2] The medial projection of the palatine appears to be unnamed although all of the other parts of this bone have been given special names. Because of the complex structure of the M. pterygoideus which originates from the palatine bone, it would be helpful if this projection also had a specific name. The most appropriate name is the medial shelf of the palatine or more simply, the palatine shelf.

the vomer and the pterygoid are of no interest to us as they are far removed from the palatine process of the premaxilla and from the muscles which may originate from it.

The fused condition of the palatine process of the premaxilla is typical for many families of passerine birds. There may be considerable variation in the relative lengths of the different processes of the palatine, but although this is of considerable importance in studies on the kinetics and functional significance of the avian skull, it is of no concern to us in this study.

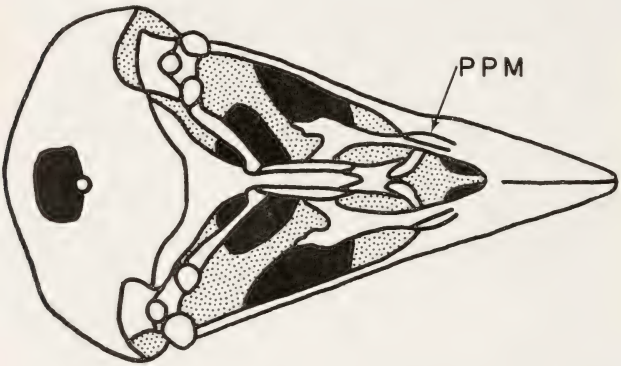

Figure 2. Ventral surface of the skull of a white-throated sparrow (*Zonotrichia*). The palatine process of the premaxilla lies along the prepalatine process of the palatine and is separated from it by a distinct suture.

Unfused palatine process. This condition of the process (called the "palato-maxillaries" by Parker, 1877, and more recently by Tordoff, (1954a, see page 374) is present in the adult stage of many genera, such as the white throated sparrow (*Zonotrichia*, Fig. 2), as a small posterior extension of the premaxilla which lies along the lateral edge of the prepalatine process of the palatine. The palatine and other bones of the skull in the white throated sparrow are similar to those of the crow and need not be described again.

There is considerable variation in the length of the palatine process and in the degree of fusion between it and the palatine in the genera possessing an unfused palatine process. Some of

this variation is a result of a difference in the age of the specimens and hence in the degree of ossification of the skull; this feature of age variation will be discussed later. In some genera, the anterior end of the palatine process degenerates, thereby destroying the connection between it and the main body of the premaxilla; the final result is an isolated splint of bone lying along the lateral edge of the prepalatine process. This isolated splint of bone may appear as if it were a new bone arising from a distinct center of ossification, but it is actually nothing more than the posterior end of the palatine process detached from

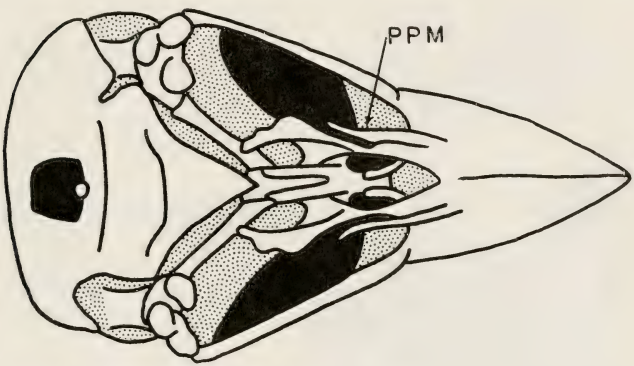

Figure 3. Ventral surface of the skull of a cardinal (*Cardinalis*). The palatine process of the premaxilla is free of the prepalatine process of the palatine and lies free in the space between the palate and the jugal bar.

the rest of the premaxilla; again, a full discussion of the development of this variant will be presented below in the section on development.

The fused condition of the palatine process may be combined with the unfused under the heading of the "normal palatine process," as found in most passerine birds.

Free palatine process. The palatine process in some groups of finches, such as the cardinal (*Cardinalis,* Fig. 3), is free of the palatine bone and lies in the space between the palate and the jugal bar. The free palatine process originates at the junction between the palatine bone and the body of the premaxilla. In some genera, there is a "suture" at the base of the free palatine process separating it from the rest of the premaxilla;

in others the palatine process continues into the rest of the premaxilla without a break (compare Figs. 31B and 31C; see also Tordoff, 1954a). The palatine and other bones of the skull are similar to those of the crow and do not require a separate description.

Lateral flange. The palatine process is lacking as a distinct structure in several groups of finches, such as the evening grosbeak (*Hesperiphona*, Fig. 4). However, in contrast to the last three types, there is a lateral flange on the anterior end of the palatine which extends almost to the jugal bar. This lateral

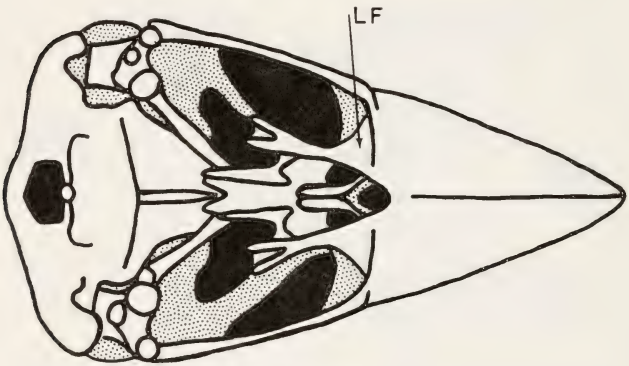

Figure 4. Ventral surface of the skull of an evening grosbeak (*Hesperiphona*). The palatine process of the premaxilla is absent (= fused to the prepalatine process of the palatine). A lateral flange is present at the site of the fused palatine process.

flange is the bony boss referred to below in the section on function and elsewhere in this paper. The lateral flange of the palatine is usually fused to the premaxillary mass, but it is sometimes separated from that bone by a suture. The palatine and other bones of the skull are similar to those described for the crow except that they are stouter and the transpalatine process is divided into two subprocesses. There is no evidence of a strengthening of "twisted" prepalatine bars such as described by Tordoff (1954a, p. 18).

HISTORY

Many of the current problems in understanding the palatine process of the premaxilla have a historical basis and thus can be fully appreciated only after one knows the history of the studies on this structure. The most important of these problems concerns the "distinction" between the palatine process and the "palato-maxillary" of Parker and of Tordoff; these terms actually refer to the same structure as will be shown below (see p. 381).

Study of the palatine process in birds began in the 1860's with the work of W. K. Parker. No other student of avian anatomy mentioned the process prior to the late 1880's. Parker clearly described and figured the palatine process of the premaxilla in all of his works including those on the palate of the "aegithognathous birds" (1875c, 1877). But, for some inexplicable reason, he stated in the description of *Tanagra cyanoptera* (1877, pp. 252-253) that: "the praemaxillary mass is . . .; the palatine processes are aborted (*d.*, *px.*, *ppx.*).

"Where the latter processes existed in the embryo, a falcate spicule of bone appears, a separate 'palato-maxillary (*p. mx.*).' This is a character to be found in several families of the Coracomorphae, as I shall soon show. Its presence suggests some delicate bond of affinity between the families where it is found." Parker then described a "palato-maxillary" instead of a palatine process of the premaxillary in the members of the New World nine-primaried oscines. The most puzzling aspect of the "palato-maxillary" is that it appears to be identical to the palatine process of the premaxilla found in other passerine families when the two structures are compared in the adult. Yet Parker never stated how one distinguished between the two bones in the adult passerine bird. Nor did he present in this paper (1877) or in any other, the evidence supporting his belief that the palatine process aborts in the embryo of the New World nine-primaried oscines and that a separate center of ossification — the "palato-maxillary" — develops to take its place. Although Parker had studied the development of the palate in many species of passerine birds, he never investigated fully the embryology of the palate in any member of the nine-primaried complex. His only mention of the development of the "palato-maxillary" is a description of one stage in the development of the skull of a cardinal. In this description, Parker said only that the "palato-maxillaries" grow in the space between the palate and the jugal bar as additional wedges (Fig. 8A). However, he did not give the age of this

specimen, nor did he have a series of specimens of different ages; hence there is no direct evidence of the palatine process aborting and a separate "palato-maxillary" taking its place. Parker did offer a very important suggestion on a possible origin of the "palato-maxillaries" in a footnote (1877, p. 263), although he did not follow it up: "The rapid development and early ankylosis of the bony centres in birds makes the study of their osteology very difficult; also the breaking off of a projection of a primary centre to make a new bone, as in the mesopterygoid. I am in some doubt whether this lateral piece of the tetramerous vomer of the type now being described is not formed in this way. Perhaps, also, in some cases, the distinct 'palato-maxillaries' may be the palatine process of the praemaxillary detached; I have, however, no proof of this; and that process is very apt to become absorbed when no palato-maxillary appears. It is sure to be removed if a new centre came in behind it to take its place." The evidence and reasoning presented here by Parker is as strong an argument for the "palato-maxillary" being the same as the palatine process as it is for the two bones being different structures. Thus it can only be concluded that Parker did not have any good evidence supporting his belief that the palatine process of the premaxilla aborts in the New World nine-primaried oscines and that a separate "palato-maxillary" takes its place. It is difficult to understand how a worker of Parker's caliber could describe a separate bone on such flimsy evidence until one realizes that he was the first worker to describe the minute processes found in the passerine skull. In his work on the development of the palate, he had only the crudest technical aids, especially stains, and could easily be misled by a poorly preserved specimen in which the posterior tip of the palatine process had broken off and resembled a separate center of ossification. The remarkable thing is that Parker was able to describe as much as he did with primitive methods and equipment.

At this point, Parker's work on the skull of the woodpeckers (1875a) should be mentioned because he described a separate "palato-maxillary" in this group, this being the first description of the structure. According to Parker, the palatine process of the premaxilla in the woodpeckers lies on the inside of the palatine and becomes fused to the medial side of that bone, not to the lateral side as in most birds. In some (all?) species of woodpeckers, there is a separate spicule of bone lying along the lateral edge of the prepalatine process, which Parker called

the "palato-maxillary." Thus if Parker's observations are correct (I have not been able to check them), there is a separate "palato-maxillary" in the woodpeckers and the term "palato-maxillary" should be used only for this structure.

Curiously enough, later workers used only the term "palato-maxillary" even when discussing the non-New World nine-primaried passerines, and extended its meaning until it became almost synonymous with the palatine process of the premaxilla. The reason for the initial confusion is obscure, but the results are clear enough — today it is impossible to determine what is meant when the term "palato-maxillary" is used.

In the years following Parker's work, the palates of a number of passerine species were described by various workers (Garrod, 1872, 1877; Forbes, 1880, 1881, 1882; and Pycraft, 1905a, 1905b, 1905c, 1907). Unfortunately, there is no indication whether these workers knew Parker's papers so that we can never be certain if the palatine process of the premaxilla was truly absent in the adult of the species described when an author failed to mention or to figure it; often the palatine process was overlooked if present, or otherwise omitted from discussion.

A number of workers did, however, describe the palatine process under several different names. Thus, Shufeldt (1888), in describing the osteology of *Pheucticus melanocephalus*, the black-headed grosbeak, stated (p. 439): ". . . the palatines on either side develop a *secondary palatine* process (sp. p., Fig. 1), extending backwards from a point to the outer side of where the anterior palatine limb fuses with the premaxillary." Later in the same paper (p. 441), he described the secondary palatine process in *Piranga* and claimed that the possession of a secondary palatine process by these birds (a tanager and a cardinaline finch) indicated an affinity between them. Apparently, Shufeldt had not seen Parker's paper on the palate of "aegithognathous birds" because his secondary palatine process is the same as Parker's "palato-maxillary." Nevertheless, the two authors agree as to the taxonomic value of this structure.

Lucas, in a series of papers (1888 to 1895), reported on the osteology of many groups of American Passeres. He did not mention the palatine process in his studies on the thrushes, the thrashers and the wrens, families in which the palatine process is usually lacking in the adult. We can be certain that Lucas had read Parker's papers for he described the palatine process (under the name "palato-maxillary") in some members of the New World nine-primaried oscines. He was, however, doubtful of its

embryological origin for he stated in his study on the osteology of the swallow-tanager (*Tersina*) (1895, pp. 505-506) that: "There is a stout palato-maxillary process, whether or not developed from a separate center is not known." In addition, Lucas questioned its taxonomic value and stated (1894, p. 304): "Its exact [taxonomic] value remains to be shown, for it appears in forms which are not related, at least closely and drops out in some that are nearly allied. It is present in the Swallows, but not in the Flycatchers or Thrushes, is well developed in such stout-billed Finches as *Cardinalis* and *Habia,* missing in *Coccothraustes.* It appears as a slender splint in *Plectrophanes* and *Calcarius,* while it is lacking in *Phoenicophilus.* None of the Drepanididae and Meliphagidae examined have a palato-maxillary." These questions posed by Lucas on the embryological origin and on the taxonomic value of the palatine process of the premaxilla, or the "palato-maxillary" as he called it, are most pertinent and have remained unanswered to the present day.

In the years between 1900 and 1950, several workers described the palatine process in a number of passerine families (Clark, 1912, 1913a, 1913b, 1913c; Lowe, 1924, 1931, 1938a, 1938b, 1947, 1949; Stonor, 1942; Sushkin, 1924, 1925, 1927, 1929), but no further contributions were made regarding its origin or taxonomic significance. Amadon, in his monograph on the Drepaniidae (1950a), included a long discussion on the "palato-maxillaries" (pp. 213-216). He stated that they are absent in the Drepaniidae, but suggested (p. 216) that the flange on the lateral side of the prepalatine bar may represent the fused "palato-maxillary." However, because of the scope of his paper, Amadon was forced to leave many questions unanswered and concluded (p. 216) that: "Little is known of the significance of the palato-maxillaries."

Tordoff's studies (1954a, 1954b) on the relationships of the "Fringillidae" and the New World nine-primaried oscines are based almost entirely on the structure and variation of the "palato-maxillaries" in these families. This work has been, up to the present, the most extensive study of the "palato-maxillaries" in any group of passerine birds and the only one that bases important taxonomic conclusions on them. Unfortunately, Tordoff did not examine families outside of the nine-primaried complex and the ploceids for the presence of "palato-maxillaries," nor did he examine the embryology of this structure. He was apparently unaware that Parker had described a very similar structure under the name "palatine process of the

premaxilla'' in other passerine families and had even suggested that the two bones might be the same. In addition, Tordoff's conclusions of the functional significance of the ''palato-maxillaries'' are decidedly different from those arrived at in this paper. Due to the evidence presented in this study, I am unable to accept Tordoff's paper.

Recently, Jollie (1958, pp. 27-28) investigated the development of the ''palato-maxillaries'' in connection with his studies on the embryology of the avian skull. He showed that the ''palato-maxillary'' is the remnant (posterior part) of the palatine process of the premaxilla and not a separate center of ossification. This is a most important contribution to the clarification of the origin of the ''palato-maxillary.'' Unfortunately, Jollie neglected to include a clear statement as to whether the term ''palato-maxillary'' is or is not synonymous with the palatine process of the premaxilla.

From this brief history of the past studies on the palatine process of the premaxilla (or the ''palato-maxillary'' as it is usually, but erroneously called), it can be seen that the available information is very limited in spite of the fact that it was described many years ago and has been studied by many workers. Therefore, it will be necessary to investigate all facets of the palatine process before its value in showing relationships within the Passeres can be ascertained.

DEVELOPMENT OF THE PALATINE PROCESS OF THE PREMAXILLA

The development of the palatine process must be known before several questions on its nature and identity with the ''palato-maxillary'' can be answered. Unfortunately, there are too few studies on the development of the skull in passerine birds and even fewer which include the development of the minor processes of the upper jaw and of the palate. The present discussion, consequently, rests almost entirely on the old but excellent studies by Parker (1872; 1873a, 1873b, and 1875b) and on the recent work by Jollie (1957 and 1958). The original contributions of the present study are meager and include only the development of the palatine process in the cardinal (*Cardinalis*), and observations on the ossification of the skull in such post-fledgling birds as are available in collections.

The following questions should be kept in mind while reading the descriptions of the development of the palatine process:

a) Is the palatine process present in the embryo of all passerine birds including those which do not exhibit a distinct palatine process as adults?

b) Is the "palato-maxillary" a separate center of ossification?

c) Is the free palatine process as seen in the adult cardinal homologous with the palatine process of other passerine birds, or is it an ossified tendon?

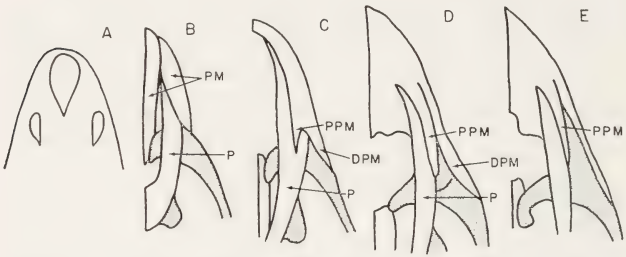

Figure 5. Series showing the development of the palatine process of the premaxilla in the crow (*Corvus*). Except for figure A which shows both halves of the skull, the figures illustrate the ventral surface of the left half of the skull. The ages of the specimens are: (A) Sixth day of incubation; (B) Ninth day of incubation; (C) Hatchling; (D) Week-old hatchling; and (E) Fledgling. The figures are redrawn from Parker (1872).

Fused palatine process. A few specimens with an unfused or a partly fused palatine process can be found in almost every large series of birds normally having the palatine process of the premaxilla completely fused with the prepalatine process in the adult (e.g., *Cyanocitta cristata,* Fig. 28F). These specimens usually show signs of immaturity, such as unossified "parietal windows." This would suggest that the palatine process is present in the young bird and becomes increasingly fused with the prepalatine process until the two bones are completely fused in the adult.

The typical course of development of the palatine process in the Passeres can be seen in the crow (*Corvus*). The following account and figures have been taken from Parker's description of the development of the skull of the crow (1872), which is still

the most complete one available for any species of passerine birds.

The premaxilla of the crow appears at about the sixth day of incubation in the form of three separate nodules of cells (Fig. 5A), the center nodule corresponding to the nasal process of the premaxilla while the lateral nodules correspond to the two halves of the main body of the bone. Neither the palatine process of the premaxilla nor the palatine have appeared by this time. By two or three days later (Fig. 5B), the nodules have enlarged and fused together to form a recognizable premaxilla. The dentary processes of the premaxilla have appeared by this time and run backwards to meet the maxillae on either side. The palatines have also appeared and are quite well developed, although the palatine processes of the premaxilla have not yet made their appearance. Parker's next stage (Fig. 5C) is a hatchling bird. The palatine processes have appeared and are small projections on the medial side of the premaxilla. They overlie the palatines. By the time the hatchling is a week old (Fig. 5D), the palatine process has enlarged to cover the lateral half of the prepalatine process. Up to the time of fledging, the palatine process continues to grow and to remain distinct from the prepalatine process (Fig. 5E). From the time of fledging or shortly thereafter, the palatine process of the premaxilla starts to fuse with the prepalatine process of the palatine until the two bones are completely fused together. There was no sign of a palatine process of the premaxilla in any of the adult crow skulls that I examined.

Among other birds possessing a fused palatine process, information on its development is available for the titmouse (Fig. 6A), the thrushes (Figs. 6B, 6C, and 6D), and the house sparrow (Fig. 7A). These species agree with the crow in possessing a distinct palatine process of the premaxilla in the embryo which becomes fused with the prepalatine process during development. The presence of a palatine process in the house sparrow (a ploceid finch) is of interest since Tordoff claimed that this group lacked "palato-maxillaries."

Unfused palatine process. The unfused condition of the palatine process, or the isolated splint lying along the prepalatine process, as seen in some of the emberizine finches, is the typical "palato-maxillary" of Parker and of Tordoff. According to Parker, the palatine process of the premaxilla aborts in the New World nine-primaried oscines and a separate center of

ossification — the "palato-maxillary"—takes its place. However, Jollie's description of the junco, an emberizine finch (Fig. 7D) shows that the development of the palatine process in this species is identical to that described for the crow except that the fusion between the palatine process and the prepalatine process does not go to completion. I have examined a fledgling towhee (*Pipilo*) which has a perfectly normal development of the palatine process similar in all respects to that seen in the junco. Thus there is no evidence supporting Parker's hypothesis that a separate center of ossification takes the place of the aborted palatine process.

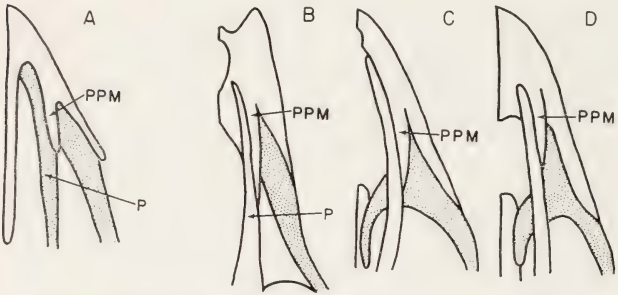

Figure 6. Development of the palatine process of the premaxilla in the titmouse (*Parus*) and the thrush (*Turdus*). Figure A shows the palatine process in a titmouse at about the tenth day of incubation; redrawn from Parker (1873a). Figures B, C, and D illustrate the palatine process in a prehatchling *Turdus viscivorus,* a day-old *T. merula,* and a week-old *T. merula* respectively; redrawn from Parker (1873b).

The isolated splint lying along the prepalatine, which some workers might consider to be the true "palato-maxillary," develops by the degeneration of the anterior end of the palatine process which thereby destroys the connection between the rest of the palatine process and the main body of the premaxilla. Jollie illustrates the development of this splint in the junco and I have seen good series of this change in *Formicarius* (Figs. 23D, 23E), *Spizixos* (Figs. 24D, 24E, 24F), *Melospiza* (Figs. 25G, 25H, 25I) and *Paradisaea* (Figs. 28G, 28H, 28I). These observations substantiate Parker's hypothesis that the "palato-maxillary" may be the posterior part of the palatine process

detached from the rest of the premaxillary, and hence not a separate bone.

Free palatine process. The palatine process of the cardinal is, in many respects reminiscent of an ossified tendon. The M. pterygoideus ventralis lateralis originates from this process by means of a tendon, and consequently, it is possible that the entire free process seen in the cardinal could be an ossified tendon which originates from the main body of the premaxilla. My suspicions of this possibility were increased by the presence in

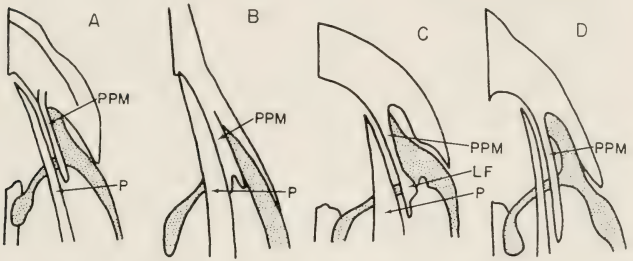

Figure 7. The palatine process of the premaxilla in: (A) A nestling house sparrow (*Passer*, redrawn from Jollie, 1958); (B) A five-day old embryo linnet (*Carduelis*, redrawn from Parker, 1875b); (C) A nestling house finch (*Carpodacus*, redrawn from Jollie, 1958): and (D) A fledgling junco (*Junco*, redrawn from Jollie, 1958).

one specimen of a faint longitudinal suture on the lateral half of the prepalatine process. This could be the suture between the semifused palatine process and the palatine if the free process seen in the adult cardinal was not the true palatine process of the premaxilla. Histological sections were prepared of the free process in the hope of ascertaining its identity. No difference could be detected between the bone of the free process and that of the premaxilla, but this result is inconclusive. Ossified tendon and bone are almost identical, if not identical, histologically. Therefore the only means of solving this problem was to study the development of the palatine process in the cardinal. Unfortunately, Parker did not give sufficient detail in his treatment on the embryology of the palate in the cardinal (see Fig. 8A) so that a series of cardinals ranging in age from hatchling to post-fledgling were gathered and stained to show the details in the

development of the palatine process. These specimens (Figs. 8B, 8C, 8D) prove that the free process in the cardinal is the true palatine process of the premaxilla and not an ossified tendon. It is possible that the tendon attaching to the free process has ossified for a short distance starting at its origin and thus has elongated the process, but this would be exceedingly difficult to verify. However, even if the free process was enlarged through ossification of the attached tendon, it would still be the palatine process. The position of the palatine process in a hatchling rose-breasted grosbeak (*Pheucticus*) also indicates that the free process in this species is the true palatine process of the premaxilla.

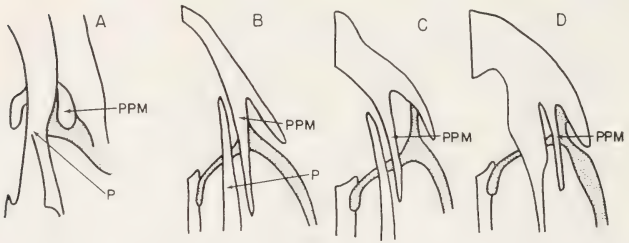

Figure 8. Development of the palatine process of the premaxilla in the cardinal (*Cardinalis*). Figure A is a bird of unknown age redrawn from Parker, 1875b. The series B, C, and D are drawn from specimens of a hatchling cardinal, a fledgling cardinal, and a post-fledgling, half-grown cardinal, respectively.

Lateral flange. Those birds, such as the carduelinе finches, which possess a lateral flange at the anterior end of the palatine, also lack a palatine process in the adult. Tordoff stated that the Carduelinae do not have a "palato-maxillary" (with the tacit assumption that it is also absent in the embryo) and are therefore related to the ploceid finches. However, Parker (1875b) shows a very distinct palatine process in the early embryo (five days) of the linnet (Fig. 7B) and Jollie (1958, p. 29) shows an equally distinct process in the house finch (Fig. 7C). Hence, the palatine process of the premaxilla is present in the embryo of the carduelinе finches and becomes fused to the palatine during development. Ossification of the lateral flange starts at the palatine process as can be seen in Jollie's figure of the house finch (Fig. 7C).

Conclusion. The palatine process of the premaxilla is present in the immature of all studied species of passerine birds and it is probably present in the immature of all passerines (see also, Jollie, 1958, p. 27, who concludes that the palatine process is probably present in the immature of all birds). It is most probable that the palatine process was overlooked in those studies (e.g., Huggins, *et al.*, 1942) in which it is not mentioned. In most passerines, the palatine process becomes indistinguishably fused with the prepalatine process of the palatine during post-hatching development. There is no indication of the palatine process aborting and a separate center of ossification taking its place in the New World nine-primaried oscines. Therefore, all of the structures in the passerine birds which have been called the "palato-maxillary" or the "secondary palatine process" are the same as the palatine process of the premaxilla; that is, these terms are synonymous. None of these structures, e.g., the free process in the cardinals, are non-homologous structures which have been misidentified as the palatine process. Lastly, it is best not to give the isolated splint lying along the prepalatine process a separate name. This procedure implies that the splint developed as a separate bone while it is nothing more than the posterior part of the palatine process detached from the main mass of the premaxilla.

FUNCTION OF THE PALATINE PROCESS OF THE PREMAXILLA

Analysis of the functional significance of most morphological systems is, by necessity, based on deductive reasoning. The functional conclusions are only hypotheses and must be treated as such. Only after these hypotheses have been tested by extensive experiments, can they be relied upon and, even then, there is a chance that some important factor has been overlooked. The deductive method of functional anatomy is based partly on a consideration of the laws of mechanics and partly on a consideration of the relative development of the structure in forms having different habits. For instance, if the shape and mass of certain jaw muscles differ between seed-eating and insect-eating birds, then the basic assumption would be that this difference is somehow associated with feeding habits. The details of the particular functions are, then, worked out using the principles of mechanics. This simple method has enabled functional anatomists to analyze highly complex systems, even though their

results are largely hypothetical. It is hoped that experimental workers will test the conclusions of functional anatomy and determine which of their conclusions and working hypotheses are correct. Such work may be most difficult from a technical standpoint, but the results would be invaluable to students of anatomy and evolution.

The palatine process of the premaxilla has three major functions which are partly independent of one another. One function is found in all passerine birds and is complementary to the two others which appear to be mutually exclusive. The first function is the insurance of a firm connection between the palate and the upper jaw, while the two mutually exclusive ones are: a point of origin for part of the M. pterygoideus, and a bony boss against which seeds are crushed. The first function may be considered to be the primary function of the palatine process and the others to be secondary ones. This division of functions into primary and secondary ones is not to be confused with original and successive functions; it is a division according to relative importance, not according to the time of appearance. A function may be defined as primary if it is the most important or the most basic function of the structure. It is present in all species possessing the structure and thus can be considered as the function responsible for the maintenance or the preservation of the structure. Secondary functions are subservient to the primary function in that their action must be in harmony with the action of the primary function. Usually secondary functions are not found in all species possessing the structure. An example of primary and secondary functions may be found in the avian wing. Active flight is generally the primary function of the wing, while display, defense, underwater swimming and so forth are secondary functions. So long as a bird must be able to fly, these secondary functions are subservient to the primary function of flight. Although the primary function is responsible for maintaining a structure, it is not necessarily responsible for the origin of that structure. A former secondary function could have become the primary function in the course of evolution and thus become responsible for the preservation of the structure. The original primary function would then become a secondary function or drop out entirely. This is the well-known phenomenon of preadaptation or functional change (*Funktionswechsel* of Dohrn, see Bock, 1959). In the example of the avian wing, active flight is currently the primary function, but it is not the original function responsible for the origin of the wing. The original function was

probably gliding which was replaced by active flight when the fore limb became sufficiently developed as a wing to acquire this new function. Similarly, underwater swimming was once a secondary function of the wing in the ancestral penguins, as it is in the auks and the diving-petrels, but became the primary functions when penguins no longer needed to fly.

The following analysis will be divided into two parts. The first will deal with the function responsible for maintaining the palatine process in birds, while the second will deal with the functions responsible for the modifications of the process during the evolution of the Passeres. Throughout the discussion, I will switch from the function to the selection force associated with that function and vice versa. In general, there is a major selection force for each function and that selection force can be described in the same terms as the function. Thus, if the function of a bony process is that of a brace to support the bone, then the selection force is for a brace to support the bone. For those who are not used to switching from function to selection force, the best way to keep the two separate is to think of the function as the static phenomenon and the selection force as the dynamic phenomenon.

Before proceeding to the discussion of the function of the palatine process, it is necessary to establish the limits of this study. The palatine process of the premaxilla is part of the extensive character complex of bones, muscles, ligaments and other structures that make up the jaw mechanism. A character complex may be defined as that group of characters that acts together as a single functional unit. A structure may belong to several character complexes, and a large complex, such as the jaw mechanism, may be divided into a number of smaller component complexes. Whenever possible, the entire character complex, not the individual component characters, should be the unit of study. A complete study of the jaw mechanism in the Passeres is most desirable and must eventually be done in order to understand the passerine feeding modifications and the relationships between groups of passerine birds (e.g., the development of the seed-cracking bill versus the relationships between the various groups of finches), but I do not have the knowledge to undertake such a study at this time. In this paper, I have restricted myself to the function of the palatine process of the premaxilla, but have included the function of such other structures as seemed pertinent to the problem.

Maintenance of the palatine process. The kinetic skull of birds with its movable upper jaw necessitates a firm connection between the palate and the upper jaw. The strength of this connection is increased by the palatine process which provides a larger surface to which the palatine can fuse. Hence, it is postulated that the primary function of the palatine process is to insure a firm connection between the palate and the upper jaw, and that the selection force associated with this function would be for a stronger connection between the palate and the upper jaw. A discussion of the mechanics of the skull can provide some

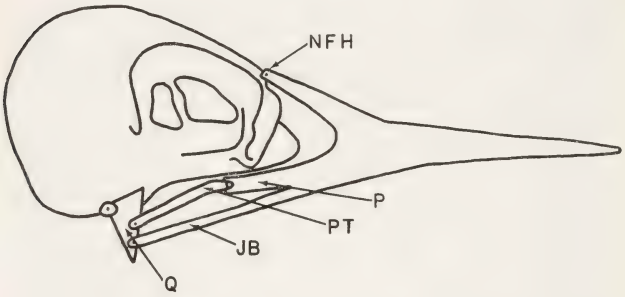

Figure 9. Diagrammatic drawing showing the mechanics of the kinetic skull in birds. When the quadrate rocks forward, it pushes on the jugal bar and the palate which in turn push on the base of the upper jaw. Because it is attached to the braincase at the nasal-frontal hinge, the upper jaw rotates upward. When the quadrate rocks backwards, the upper jaw rotates downward. Redrawn from Engels, 1940.

evidence supporting this hypothesis. I will only outline the salient features of this mechanism and refer the interested reader to Beecher's excellent discussion of the mechanics involved in elevating and depressing the upper jaw in birds (1951a, pp. 412-416).

The upper jaw of birds is not solidly fused to the braincase as in mammals and in some reptiles, but can be raised and lowered by means of a complex mechanism of bones (Fig. 9). Rotation of the upper jaw is about the nasal-frontal hinge — the connection between the upper jaw and the braincase. At its ventro-posterior end, the upper jaw is attached to the jugal bars laterally and to the palate medially. These elements connect the upper

jaw to the quadrate. All parts of this system except for the nasal-frontal hinge are free of the braincase and can move relative to it. Thus, as the quadrate rocks forward, it pushes the base of the upper jaw forward. The upper jaw, being attached to the braincase at the nasal-frontal hinge, rotates upward (Fig. 10). When the quadrate rocks backwards, it pulls the base of the upper jaw backwards and thus depresses the upper jaw. Because the muscles operating this system insert on the quadrate and the pterygoid, their force must be transmitted to the upper jaw by means of the palate and the jugal bars. The push that raises the upper jaw is probably transmitted to it only through the palate because the thin jugal bars would bend if a push was exerted on them. The pull could be transmitted through the palate and the jugal bars; however, it seems likely that most of the pull is along the palate. Hence, in addition to other factors, the proper functioning of this kinetic system is dependent upon a strong connection between the palatines and the premaxilla.

At least two important functions are achieved by the kinetic skull of birds. First, it permits a wider gape than a stationary upper jaw; this feature is desirable in such birds as the swallows and the flycatchers, which need a wide gape. Second, it preserves the primary orientation of the skull (see Moller, 1931, p. 146; Beecher, 1951a, pp. 414-415) by allowing the bird to open its bill without shifting the position of the eye with reference to the prey or "leading" the prey (Fig. 10). If the axis of the skull shifted when the bird opened its bill to capture its prey, the entire orientation of the head and neck in respect to the prey would be destroyed. The bird would have to re-orient completely in the brief instant between bill-opening and prey-capture. Development of the elaborate nervous mechanism needed for this rapid re-orientation would be difficult. It would be far easier to preserve the orientation of the skull by mechanical means, e.g., a kinetic skull. Evolution in birds has followed the latter course. The importance of these functions is indicated by the fact that almost all birds possess a kinetic skull. Hence there would be a strong selection force favoring all parts of the kinetic skull, including a firm connection between the upper jaw and the palate. It was postulated above that the palatine process of the premaxilla serves to increase the contact and presumably the degree of fusion between the premaxilla and the prepalatine process of the palatine; thus the palatine process would be favored by the selection force for the kinetic skull. Therefore, it can be concluded that the selection forces favoring the kinetic

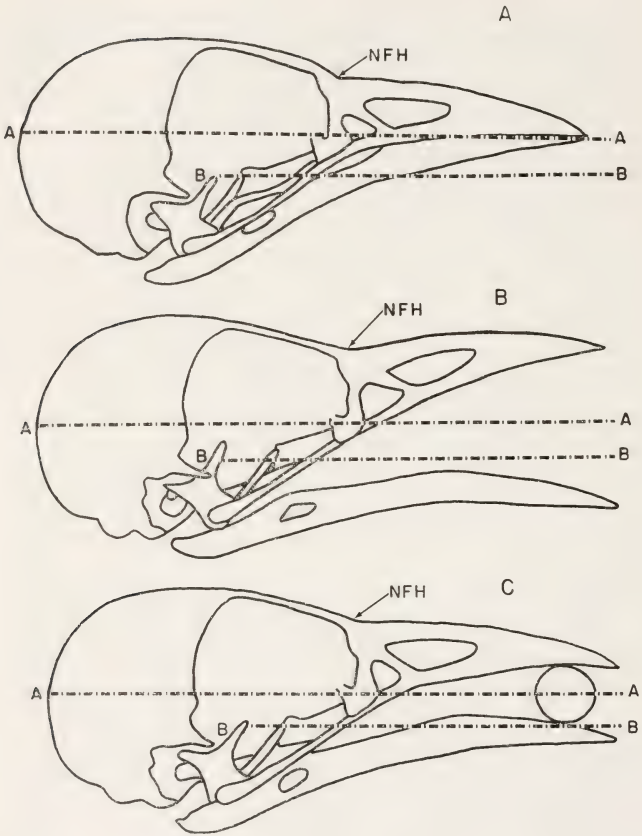

Figure 10. Diagrammatic drawings of the avian skull illustrating how the kinetic upper jaw preserves the primary axis of the skull, i.e., the position of the eyes in respect to the prey. Line A-A represents the primary axis of the skull; it lies along the gonys (the junction between the upper and lower jaws) as shown in figure A. The primary axis remains stationary and midway between the jaws when the bill opens (Figure B) and closes on the prey (Figure C). Line B-B represents the secondary axis of the skull when the bill opens if the upper jaw is not movable. Figures redrawn from Moller, 1931.

skull are responsible for maintaining the palatine process of the premaxilla in birds.

It should not be assumed that the palatine process of the premaxilla appeared as a new structure in the passerine birds. The palatine process had doubtless originated at the time birds evolved from reptiles, if not before. The palatine in most reptiles abuts against the maxilla and the vomer anteriorly and against the pterygoid posteriorly. In birds, the anterior connection of the palatine is with the premaxilla and perhaps with the maxilla by means of secondary ossification. The connection with the vomer is medial and more posterior than in the reptiles while the connection with the pterygoid is posterior as usual. The shift of the palatine from the maxilla to the premaxilla probably required the development of a point of abutment or anchorage on the premaxilla. This is the palatine process of the premaxilla. It is not known whether the shift of the palatine was associated with the development of the kinetic skull in birds because the palates of neither the pseudosuchians nor *Archaeopteryx* are known. The kinetic skull evolved sometime after the *Archaeopteryx*-stage in the evolution of birds. Nevertheless, once birds possessed a kinetic skull and a palatine process of the premaxilla, the palatine process was preserved because of the selection forces associated with the kinetic skull. It was thus available (preadapted) for other selection forces which arose during the subsequent evolution of the passerine birds.

Modifications of the palatine process. Modifications in the structure of the palatine process of the premaxilla in the Passeres have developed under the control of the several secondary functions of this structure. These will be discussed with three problems in mind. (a) Changes in the palatine process associated with modifications in the M. pterygoideus. These changes arose in connection with the development of a free palatine process, such as is found in the cardinal. (b) Development of a bony boss at the anterior end of the palatine. This is associated with the development of the lateral flange on the anterior end of the palatine in the cardueline and other finches. (c) The variation in the degree of fusion between the palatine process of the premaxilla and the palatine, and the variation in the development of the isolated splint lying along the palatines as seen in the emberizine finches.

These are not sharply separated problems, but are all interrelated under the general heading of adaptive modifications in the bill for seed-eating. I shall, therefore, first describe the

various functional mechanisms of the avian jaw which are prerequisite for understanding the modifications in the palatine process of the premaxilla and, then, under the heading of conclusions, return to these questions and answer them as best I can. Discussion of the functional mechanisms will be in the following order: first, the structure, function and variation of the M. pterygoideus in the Passeres; second, a comparison of the adaptive pathways through which the strength of the bite can be increased; third and last, a comparison of the jaw muscles and seed-cracking methods in the several groups of finches.

The M. pterygoideus. Tordoff (1954a, p. 12) assumed that the origin and evolution of the palatine process of the premaxilla (his "palato-maxillary") was dependent upon changes in the mass of the M. pterygoideus. However, he apparently only examined the jaw muscles of the cardinal (*Cardinalis*) and extrapolated the correlation between the palatine process and the M. pterygoideus in the other New World nine-primaried oscines from the condition seen in the cardinal. To be sure, part of the M. pterygoideus originates from the palatine process in the cardinal, yet it is necessary to survey the jaw musculature in the Passeres and to correlate the changes in the M. pterygoideus with the modifications in the palatine process before any statements about the evolution of the palatine process can be made. It can be stated in advance that the M. pterygoideus is the only jaw muscle that originates from the palatine process of the premaxilla.

Dissection of the M. pterygoideus is rather difficult because of the incomplete separation of the muscle into four parts and the complex arrangement of the muscle fibers. Much care must be taken to separate the parts correctly and to determine the direction of the muscle fibers in each part. The M. pterygoideus is usually divided into a ventral and a dorsal portion and each portion is, in turn, divided into a lateral and a medial half (Lakjer, 1926, pp. 65-67). Some workers (e.g. Engels, 1940, pp. 359-361) do not recognize any subdivisions of the M. pterygoideus because they cannot separate the parts with complete certainty. It is true that the subdivisions of the M. pterygoideus are not clearly defined units, but it is not necessary for the parts of a muscle to be sharply separated from one another before they are recognized as separate units. If the parts of a muscle, such as the M. pterygoideus, have different functions and are unequally developed in different forms, then they are best recognized even if they are not sharply separated from one another. It should

be emphasized that the functional unit of a muscle is not the whole muscle, or a recognizable part thereof, or even a muscle fiber, but the motor unit — which is the aggregate of muscle fibers innervated by a single nerve fiber (= motor cell axon). If we wish to be completely precise in our studies of muscle function, then we must separate the muscle into its motor units, which is an impossible task. Therefore, the degree of analytical precision is not noticeably reduced if the recognized subdivisions of a muscle merge into one another.

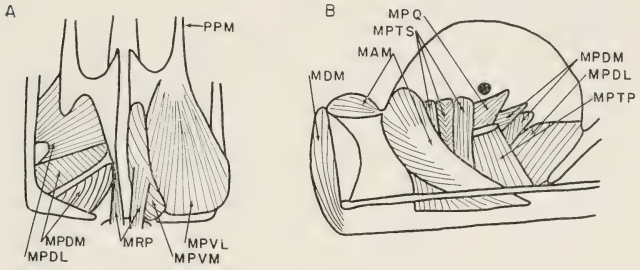

Figure 11. Jaw muscles of the gray jay (*Perisoreus canadensis*). (A) Ventral view of the M. pterygoideus. (B) Oblique view into the orbit showing the dorsal jaw muscles and the dorsal aspect of the M. pterygoideus. In the ventral view of the jaw muscles of this and all other species, the posterior end of the palatine process of the premaxilla or a point on the palatine posterior to the palatine process is indicated by an arrow (PPM). Thus the reader can note the relationship between the palatine process and the M. pterygoideus ventralis lateralis. In the gray jay, for example, there is no connection between the palatine process and the M. p. ventralis lateralis.

The following description of the M. pterygoideus (Fig. 11) is for the gray jay (*Perisoreus canadensis*), a bird having a medium-sized bill of fairly generalized shape. I shall regard the arrangement of the M. pterygoideus in this species as "typical" for the Passeres.

a) M. pterygoideus ventralis lateralis. This large segment comprises almost all of the ventral portion of the M. pterygoideus. It originates from the entire ventral surface of the transpalatine process and from much of the ventral surface of the medial shelf of the palatine, and inserts on the medial and ventral surfaces of the mandible and on the medial process of the

mandible ("internal articular process" of some authors). Both the origin and insertion of this muscle are fleshy. The M. p. ventralis lateralis is a fan-shaped muscle with some of its medial fibers inserting on the M. p. ventralis medialis. It is important to note that in the gray jay, the origin of the M. p. ventralis lateralis is from the transpalatine process and the medial shelf and not from the region of the fused palatine process of the premaxilla; that is, there is no association between this muscle and the palatine process. The M. p. ventralis lateralis is, however, the part of the M. pterygoideus that may take origin from the palatine process of the premaxilla in some groups of passerine birds.

b) M. pterygoideus ventralis medialis. This small subdivision of the M. pterygoideus comprises only a minor part of the ventral portion of the muscle and is frequently difficult to separate from the lateral part. It originates from the lateral side and from the tip of the mediopalatine process, and inserts on the distal end of the medial process of the mandible. Both the origin and the insertion are fleshy and the fibers are parallel to one another. Because of its position, the M. p. ventralis medialis is never associated with the palatine process of the premaxilla.

c) M. pterygoideus dorsalis lateralis. This large segment of the dorsal part of the M. pterygoideus lies directly over the slightly larger M. p. ventralis lateralis; only in some of the heavy-billed finches is the M. p. ventralis lateralis smaller than the M. p. dorsalis lateralis. It takes origin from the dorsal surface of the transpalatine process and the medial shelf of the palatine, and inserts on the medial side of the mandible just dorsal to the insertion of the M. p. ventralis lateralis. The muscle fibers appear to be parallel to one another and to run obliquely backwards from their origin to their insertion.[1] Except for a small aponeurosis at the corner between the mandible and its medial process, the origin and insertion of this muscle are fleshy in the gray jay; in some birds, they are quite tendinous. In the gray jay, the origin of the M. p. dorsalis lateralis is limited to the posterior part of the palatine and is far removed from the fused palatine process. However, in some passerine birds, the origin

[1] Actually these fibers are not parallel, but are pinnate for they insert on a membrane that runs along the dorsal side of the muscle rather than directly on the mandible. Pfuhl (1936) stresses this problem of the true pinnate nature of some apparent parallel-fibered muscles, but for simplicity I shall regard pinnate muscles of the M. p. dorsalis lateralis type as parallel-fibered. I realize that this is incorrect and that someday a correct description of these muscles must be given, but this simplifying assumption will not affect the results of the present paper.

of the M. p. dorsalis lateralis extends forward along the palatine as far as the premaxilla. In these groups, the origin of this anterior extension of the M. p. dorsalis lateralis is usually from the dorsal surface of the prepalatine process. But in those few groups where it takes origin from the lateral edge of the prepalatine process, the M. p. dorsalis lateralis is not associated with the palatine process of the premaxilla.

d) M. pterygoideus dorsalis medialis. This is the most sharply defined part of the M. pterygoideus. It takes origin from both sides of the pterygoid bone and from a small part of the posterior tip of the mediopalatine process, and inserts on the distal tip of the medial process of the mandible. The pterygoid divides this muscle into an anterior and a posterior part. The anterior fibers are pinnate, inserting on a tendon that runs along the anterior edge of the muscle; the posterior fibers are parallel. Except for the insertion of the anterior fibers, the origin and insertion of this muscle are fleshy. Because of its medial position, the M. pterygoideus dorsalis medialis is never associated with the palatine process of the premaxilla.

e) "M. retractor palatini." The "M. retractor palatini" is not a separate muscle as listed by some workers, but is part of the M. pterygoideus. In most passerine birds, some of the medial fibers of the M. pterygoideus run directly backward and insert on the basitemporal plate instead of on the distal tip of the medial process of the mandible. In the gray jay, a few fibers appear to take origin from the middle of the M. p. ventralis medialis and insert on the basitemporal plate. These fibers, which form a very thin layer of tissue in the gray jay, are homologous with a band of fibers in such groups as the thrashers and the thrushes that originate on the medial shelf of the palatine next to the M. p. ventralis lateralis and pass over the M. p. ventralis medialis to insert on the basitemporal plate. These fibers are probably part of the M. p. ventralis medialis although they appear to be associated with the M. p. ventralis lateralis. (I shall discuss this group of fibers in more detail below, p. 396). In addition to these ventral fibers, a small group of fibers run back from the posterior tip of the mediopalatine process to insert on the basitemporal plate dorsal to the insertion of the ventral fibers. The fibers that insert on the basitemporal plate may be grouped together as a part of the M. pterygoideus or they may be included as part of the M. p. dorsalis medialis or the M. p. ventralis medialis according to their position. I will identify them on the figures as the "M. retractor palatini," but will consider them as part of the medial

portion of the M. pterygoideus in functional discussions. The fibers of the "M. retractor palatini" are never associated with the palatine process because of their extreme medial position.

Function of the M. pterygoideus. The action of the M. pterygoideus is usually described as raising the lower jaw and lowering the upper jaw; however, this is not precise enough for the purposes of this paper. Presumably, each of the four parts of the M. pterygoideus has its own innervation and can contract independently of the others. Also, only one part may enlarge to meet the demands of a particular selection force. If all four parts of the M. pterygoideus had the same function, then one would expect that the whole muscle would evolve as a unit. Certainly then, it can be assumed that, although the action of the M. pterygoideus is to close the bill, the exact role of each of its four parts in closing the bill differs and must be determined. The following discussion is an attempt to ascertain the action of each part of the M. pterygoideus from an analysis of their origins and insertions, the directions of their muscle fibers, and their relative development in different types of birds.

The parts of the M. pterygoideus which serve to raise the mandible must be so oriented that their pull causes the depressed mandible to swing upward about its quadrate articulation. To envision the direction of these muscle fibers, one must consider the mandible and the M. pterygoideus from their lateral side as well as from their ventral side. Two groups of fibers possess the qualifications for raising the mandible. The first are those fibers originating from the lateral side of the palate, the transpalatine process and the palatine shelf and inserting on the medial side of the ventral edge of the mandible anterior to its articulation. These fibers draw the mandible directly upward and would be effective even with the bill almost closed. The second group of fibers are those which originate from the transpalatine process and the palatine shelf and insert on the medial process of the mandible, usually on its anterior face but sometimes along the ventral edge of its posterior face. These fibers pull the medial process of the mandible forward and thereby raise the mandible. When the mandible is depressed, the medial process is slightly posterior and ventral to its position when the bill is closed. The difference between the normal and the depressed position of the medial process is very small, perhaps only $\frac{1}{10}$ of the distance between the posterior tip of the transpalatine process and the medial process of the mandible when the bill is closed. This means that a slight movement of the medial process toward its

normal position results in the mandible being raised over a considerable distance. Because of their insertion near the quadrate hinge, these fibers raise the mandible rapidly, but with little power. The medial process reaches its final position when the bill is about half closed. Thus, the fibers of this second group are effective in raising the mandible only when the bill is wide open and can no longer serve in this connection after the bill is half closed. Lastly, it should be mentioned that those fibers which insert along the ventral edge of the posterior face of the medial process rotate the process and thereby raise the mandible. These fibers may be effective in raising the mandible until the bill is almost closed; however, I have not studied this point in detail.

Lowering of the upper jaw would depend upon the ability of the M. pterygoideus to retract the palate. Probably all of the fibers of this muscle, no matter what their origin and insertion might be, would draw the palate backward. However, those fibers which run obliquely from the palate to the medial side of the mandible exert only a slight backward pull on the palate. The fibers which retract the palate most effectively are those that originate on the posterior part of the palate and run directly back to insert on the medial process of the mandible. Those particular fibers which insert on the basitemporal plate can only retract the palate; they cannot have any effect on the mandible. Lastly, the fibers which originate from the pterygoid probably have as their only action, the lowering of the upper jaw.

With these background remarks in mind, the following actions may be suggested for the parts of the M. pterygoideus.

a) M. p. ventralis lateralis. The lateral fibers of this muscle act mainly to raise the mandible. The medial fibers, which insert on the medial process of the mandible, retract the palate and thus depress the mandible during their entire contraction cycle, but can serve to raise the mandible only when the bill is about half closed. In the insect-eaters, the M. p. ventralis lateralis is probably more important as a palatine retractor, but in the large-billed seed-eaters, this muscle is probably more important as an adductor of the mandible.

b) M. p. ventralis medialis. This muscle, by virtue of its origin on the mediopalatine process and its insertion on the distal tip of the medial process of the mandible and the basitemporal plate, has as its major and probably only action, the retraction of the palate. It may be noted that those birds which need large palate retractors, such as the swallows and the flycatchers, have a large M. p. ventralis medialis. I include those fibers which

originate on the palatine next to the M. p. ventralis and pass over the M. p. ventralis medialis to insert on the basitemporal plate (see drawing of the thrasher, Figs. 13A and 13B) as part of the M. p. ventralis medialis; their function is, of course, palatine retraction.

c) M. p. dorsalis lateralis. All of the fibers of this muscle run obliquely from the palatine bone to the medial side of the mandible. Thus, the action of this muscle is to raise the mandible with, at most, a very minor part of the force used to retract the palate. It could be noted that this muscle is small in insect-eaters and greatly enlarged in seed-eaters.

d) M. p. dorsalis medialis. This muscle takes origin from the pterygoid and the posterior end of the mediopalatine process and inserts on the distal end of the medial process of the mandible and the basitemporal plate; hence its sole action is retraction of the palate.

To recapitulate, the major function of the medial parts of the M. pterygoideus is to retract the palate and hence depress the upper jaw, while the major function of the lateral parts is to raise the lower jaw. The medial fibers of the M. p. ventralis lateralis can raise the mandible only during the early part of their contraction while they can retract the palate during all of their contraction. This separation of functions between parts of the M. pterygoideus is not a sharp one, for it seems likely that each part of the muscle has at least a small role in both functions. However, this division of labor between the parts of the M. pterygoideus is clearly reflected in their relative sizes in different types of passerine birds, as for example, insect-eaters as compared to seed-eaters.

Variation of the M. pterygoideus in the Passeres. The results of a survey of the M. pterygoideus in the Passeres will be reported in this section. This survey is far from complete, but it does include a number of different types of passerine birds and is, I believe, adequate for the purposes of this paper. The muscle will not be described in detail as has been done for the gray jay; instead, its ventral aspect will be figured for each species available. In the figure, the posterior end of the palatine process will be indicated to allow the reader to determine the relationship between the M. p. ventralis lateralis and the palatine process. A word of warning should be given. First, my drawings are crude representations of the very complex system of jaw muscles. I have tried to show the spatial relationships of the muscles and the directions of the fibers; however, I cannot vouch for the accuracy of the proportions or the perspective. These

figures were drawn to illustrate the points discussed in this paper and should not be used to illustrate any other aspect of the jaw muscles. Second, the style of each author differs; thus much of the difference in the jaw muscles in a bird as shown by Engels or Fiedler or myself is artificial. The significance of this survey in relation to the functional significance and evolution of the palatine process will be discussed in the conclusion of this section.

The method used in dissecting the M. pterygoideus was simply to remove the hyoid apparatus and associated muscles, to cut off the mandible just anterior to the insertion of the M. pterygoideus, and lastly to remove the lining on the roof of the mouth plus the horny covering of the upper jaw. Usually the eye was also removed to allow examination of the other jaw muscles and the dorsal aspect of the M. pterygoideus. The M. pterygoideus is now exposed and after some cleaning up of connective tissue and blood vessels, it is ready for study. Some care must be taken when removing the lining of the mouth and the horny palate to make certain that the tendons and muscle fibers in the region of the prepalatine process are not damaged or destroyed.

The following species are available for comparison:

Tyrannidae	*Tyrannus dominicensis*	Figure 12A
Alaudidae	*Eremophila alpestris*	" 12C and 12D
Hirundinidae	*Iridoprocne bicolor*	" 12B
Bombycillidae	*Bombycilla cedrorum*	" 12E
Troglodytidae	*Heleodytes brunneicapillus*	" 12F
Mimidae	*Toxostoma redivivum*	" 13A
	Toxostoma rufum	" 13B
	Nesomimus macdonaldi	" 13C
	Dumetella carolinensis	" 13D
Turdinae	*Turdus philomelos*	" 13E
	Turdus migratorius	" 13F
	Hylocichla sp.	" 14A
Paradoxornithinae	*Paradoxornis* sp.	" 14B
Polioptilinae	*Polioptila caerulea*	" 14D
Sylviinae	*Regulus calendula*	" 14C
Paridae	*Parus bicolor*	" 14E
Sittidae	*Sitta europaea*	" 14F
Nectariniidae	*Cinnyris chalybaeus*	" 15A
Zosteropidae	*Zosterops annulosa*	" 15B
Meliphagidae	*Anthornis melanura*	" 15C
Emberizinae	*Emberiza citrinella*	" 15D
	Passerella iliaca	" 15E and 15F
	Melospiza melodia	" 17A

Emberizinae (cont'd)	*Spizella pusilla*	Figure	16A and 16B
	Pipilo erythrophthalmus	"	16E and 16F
	Zonotrichia albicollis	"	16C and 16D
Cardinalinae	*Cardinalis cardinalis*	"	17E and 17F
	Passerina cyanea	"	17C and 17D
Tanagrinae	*Piranga rubra*	"	17B
Coerebinae	*Dacnis cayana*	"	19B
Parulidae	*Seiurus aurocapillus*	"	18C and 18D
Vireonidae	*Vireo olivaceus*	"	18A and 18B
Icteridae	*Molothrus ater*	"	18E and 18F
	Quiscalus quiscala	"	19A
Fringillinae	*Fringilla coelebs*	"	19C and 19D
Carduelinae	*Spinus tristis*	"	19E and 19F
	Carpodacus purpureus	"	20C
	Hesperiphona vespertina	"	20A and 20B
	Carduelis carduelis	"	20D
	Pinicola enucleator	"	20E
	Loxia curvirostra	"	20F
	Coccothraustes coccothraustes	"	21A
Estrildidae	*Lonchura orizivora*	"	21B
Ploceidae	*Passer domesticus*	"	21C and 21D
Sturnidae	*Sturnus vulgaris*	"	21E
Corvidae	*Corvus crassirostris*	"	21F
	Perisoreus canadensis	"	11

Some comparative notes on the structure of the M. pterygoideus can be given at this point. It has already been pointed out that, in the seed-eaters, the medial parts of this muscle are relatively small while the lateral parts are relatively large. In the insect-eaters, the medial parts are relatively large, although they are still smaller in mass than the lateral parts of the M. pterygoideus; the M. p. ventralis lateralis makes up a major share of the total mass of the muscle. For example, the M. p. dorsalis lateralis is very small in the kinglet (*Regulus*) and the gnatcatcher (*Polioptila*), while the medial parts of the M. pterygoideus comprise only about 5 per cent of the total muscle mass in such heavy-billed finches as the evening grosbeak (*Hesperiphona*). The structure of the "M. retractor palatini" in the Old World insect-eaters, such as the kinglet, thrushes, thrashers and wrens, is very characteristic. The dorsal band of fibers originates along with the M. p. dorsalis medialis from the distal tip of the mediopalatine process, and is unquestionably part of that muscle. The ventral band of fibers originates from the palatine shelf next to the M. p. ventralis lateralis and passes over the M. p. ventralis medialis before inserting on the basitemporal plate. Although these fibers appear to be part of the

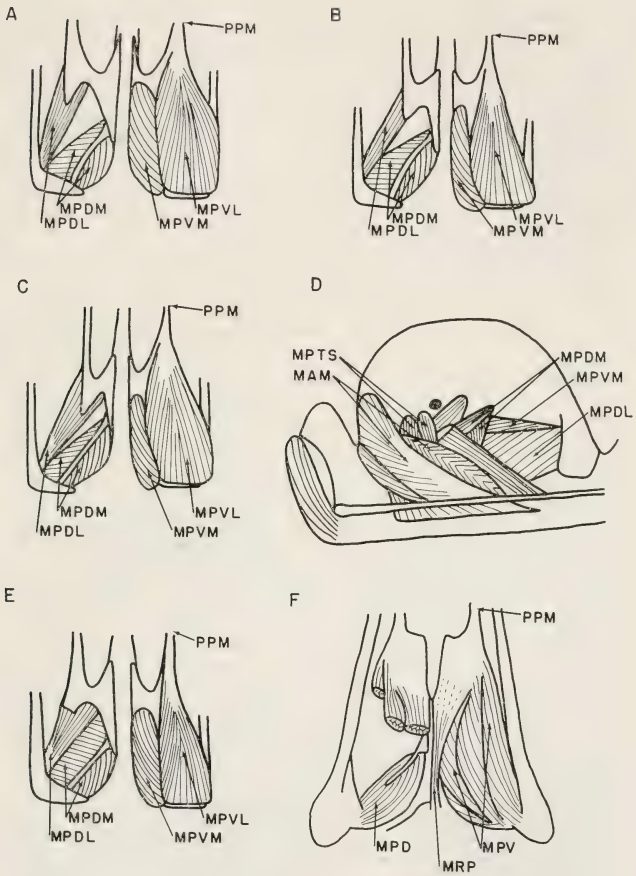

Figure 12. Jaw muscles of: (A) *Tyrannus*; (B) *Iridoprocne*; (C and D) *Eremophila*; (E) *Bombycilla*; and (F) *Heleodytes* (redrawn from Engels, 1940).

M. p. v. lateralis, they are most probably part of the M. p. v. medialis. They may have at first originated from the ventral edge of the mediopalatine process along with the rest of the M. p. v. medialis and then moved laterally to the palatine shelf as their mass increased. It is possible that these fibers are part of the M. p. v. lateralis and that their insertion shifted from the medial process of the mandible to the basitemporal plate, but this does not seem probable. A more thorough study of the innervation of these fibers is needed before we can be certain of their origin.

Beecher (1951a, 1953) illustrated the dorsal aspect of the M. pterygoideus and identified four subdivisions — the M. p. dorsalis anterior, M. p. dorsalis posterior, M. p. ventralis anterior and M. p. ventralis posterior (Beecher's terminology). Most of his figures (1953) show the usual four subdivisions, but some (sunbird, p. 291; white-eye, p. 291; wood warbler, p. 306; see Fig. 22B; and wren, p. 318) show five subdivisions (the identity of the fifth subdivision is usually not mentioned) and others show only three subdivisions. In the case of birds with only three parts of the M. pterygoideus visible through the orbit, these parts are always the M. p. d. anterior, M. p. d. posterior and the M. p. v. anterior, as for example, in the house finch, the cowbird (Fig. 22D) and the song sparrow (Fig. 22C). In the latter species, there can be no doubt of Beecher's identification of the M. p. v. anterior for he states (1953, p. 307) that: "Large M. 4a [= M. p. v. anterior] overlying M. 4b [= M. p. v. posterior]." Yet my dissections of the finches revealed that the origin of the M. p. dorsalis lateralis extended anteriorly along the prepalatine process as far as the premaxilla in some species (see also, Fiedler, 1951; and Sims, 1955, p. 381). In these birds, the M. p. ventralis would be completely covered by the M. p. dorsalis and invisible when the jaw muscles are viewed through the orbit. Dissection of other passerine birds showed that the M. p. dorsalis lateralis covers much of the M. p. ventralis lateralis and that the M. p. ventralis medialis is usually not visible when the muscles are viewed through the orbit. Only in the thin-billed species can much of the ventral portions of the M. pterygoideus — usually the M. p. ventralis lateralis— be seen when the dorsal aspect of this muscle is examined through the orbit. In any case, the ventral parts of the M. pterygoideus are visible between the two dorsal parts of this muscle, not lateral to both dorsal segments as shown by Beecher. Consequently, his identifications of the parts of the M. pterygoideus would seem to be wrong and should

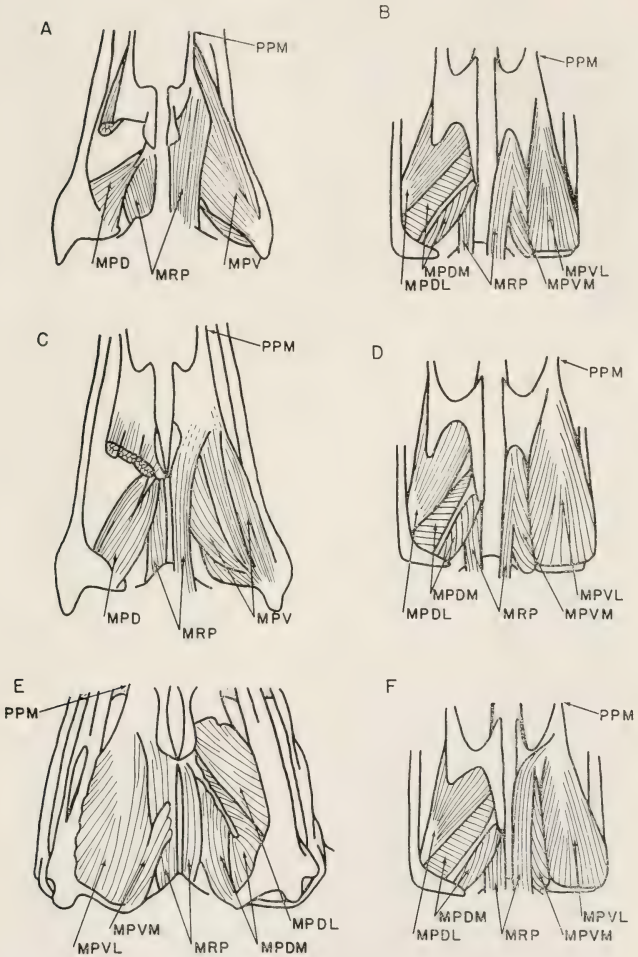

Figure 13. Jaw muscles of: (A) *Toxostoma redivivum* (redrawn from Engels, 1940); (B) *Toxostoma rufum*; (C) *Nesomimus* (redrawn from Engels, 1940); (D) *Dumetella*; (E) *Turdus* (redrawn from Fiedler, 1951); and (F) *Turdus migratorius*.

be corrected. His M. p. dorsalis anterior and M. p. d. posterior are the two parts of the M. p. dorsalis medialis which are anterior and posterior to the pterygoid respectively. His M. p. ventralis anterior is the M. p. dorsalis lateralis. Thus, his M. p. ventralis posterior would be part of the M. p. ventralis and most likely the M. p. ventralis lateralis. The fifth portion shown in some figures would be the M. p. ventralis medialis. However, there is some doubt as to the identification of the ventral parts of the M. pterygoideus shown in Beecher's figures. In some cases, his M. p. ventralis posterior may be the M. p. ventralis medialis instead of the M. p. v. lateralis, or, more likely, two muscles should have been shown instead of just one. I may add, at this point, that the only way to be certain of the identification of the parts of the M. pterygoideus is to dissect them from the ventral side of the muscle. These misidentifications and the tacit assumption that the M. pterygoideus only retracts the palate invalidate Beecher's remarks on the structure and the function of the M. pterygoideus.

Here may be the best place to interject a few comments on the factual parts of Beecher's work as there are a number of discrepancies between his drawings and my dissections of the same bird or a species within the same family. For example, Beecher shows the medial slip of the M. adductor mandibulae in the larks (1953, p. 316) as a parallel-fibered muscle, but in my dissection of the same species, this muscle was complexly pinnate. Again, Beecher shows the same muscle slip in the Icteridae as pinnate (1953, p. 308), although he showed it as parallel-fibered in his earlier paper (1951a). My dissections of several genera of the Icteridae, including the cowbird, agree with his earlier paper. In both his dissections and drawings, Beecher studied only the external aspect of the muscles and did not dissect the muscles themselves, nor did he attempt to ascertain the mass or cross-sectional area of the muscles. Thus a muscle is considered to be important if it exhibits a large surface area as shown in his drawings. All pinnate muscles are lumped together as one type and automatically considered to be better and more efficient than parallel-fibered muscles. Aside from these points, there are many interpretations which do not seem to agree with the facts presented. For example, the drawings of the adductor (= medial) slip of the M. adductor mandibulae do not agree with his separation of the oscine families into two superfamilies on the basis of a pinnate slip in the one group and a parallel-fibered slip in the other group. Nor can I understand the evolu-

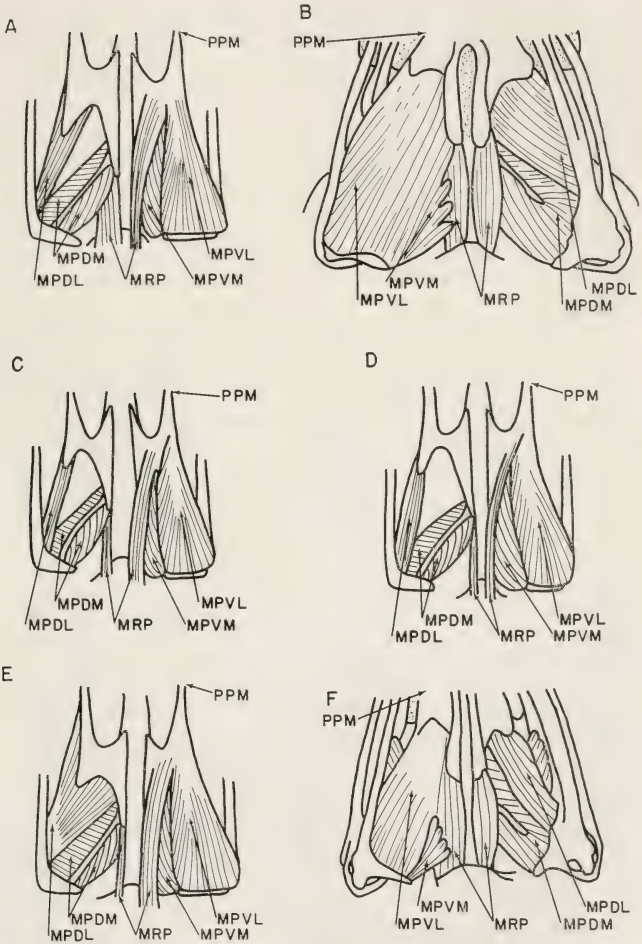

Figure 14. Jaw muscles of: (A) *Hylocichla*; (B) *Paradoxornis* (redrawn from Fiedler, 1951); (C) *Regulus;* (D) *Polioptila;* (E) *Parus;* and (F) *Sitta* (redrawn from Fiedler, 1951).

tionary shift of the muscle fibers from the M. adductor mandibulae to the M. pseudotemporalis superficialis (Beecher, 1951b, p. 278). However, Beecher's functional discussions are excellent and should be read by those interested in the functional anatomy of the avian skull.

Yet, this critical evaluation of Beecher's work should not be interpreted as meaning that the jaw muscles cannot supply good clues to the relationships and evolution of the passerine birds. They may well prove to be useful if analyzed with extreme caution and with the realization that they are subject to the same evolutionary phenomena, such as convergence, that make the study of any taxonomic character difficult (see also Starck, 1959).

Comparison of the adaptive pathways for increased force of the bite in the passerine birds. I have mentioned above that the major modifications of the palatine process in the passerine birds appear to be associated with the functional demands of seed-eating. However, the relationship between seed-eating and the structure of the palatine process is not a simple one such as the free palatine process (cardinal condition) becoming more and more fused as the M. pterygoideus decreases in size (Tordoff, 1954a, p. 12) and vice versa. If this were true, then why do the heavy-billed cardueline finches lack the free palatine process and possess lateral flanges on the anterior end of the prepalatine processes? This question leads to the fundamental question of the entire problem: What are the basic requirements for seed-eating, and how have passerine birds evolved the necessary structural adaptations to meet these demands?

Aside from behavioral traits and such morphological features as the length of the gut (see Eber, 1956), the necessary digestive enzymes and so forth, the basic requirement of a seed-eating bird is to be able to crack the hard shell of a seed without damage to itself. One way to meet this requirement is to grind the seeds in the muscular gizzard, as done by gallinaceous birds and pigeons. Passerine birds have not utilized this method, but crack seeds by means of a powerful closing of their bill. Thus, seed-eating passerines must be able to crack seeds in their bill without damaging the structures of the head, especially the brain and sense organs. Larks are apparently an exception for they swallow seeds whole and grind them in their gizzard (Meinertzhagen, 1951, p. 84). The central problem of this section is, therefore: What are the ways by which a passerine bird might increase the strength of its bite and at the same time protect the

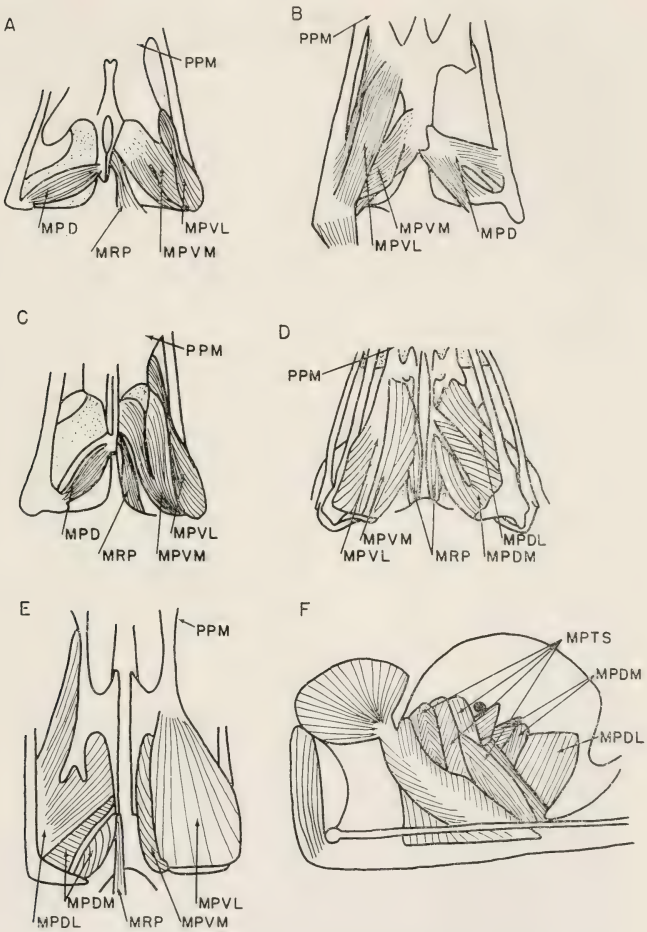

Figure 15. Jaw muscles of: (A) *Cinnyris* (redrawn from Moller, 1930); (B) *Zosterops* (redrawn from Moller, 1931); (C) *Anthornis* (redrawn from Moller, 1931); (D) *Emberiza* (redrawn from Fiedler, 1951); and (E and F) *Passerella*.

other structures of its head against the forces and shocks associated with seed-cracking? The several methods by which the strength of the bite can be increased will be described first, and then it will be shown how different combinations of these methods have evolved in the several groups of finches.

Muscles that close the bill. Four separate jaw muscles in the Passeres act to close the bill, either by raising the mandible or by depressing the upper jaw. Increase in the mass of any of these muscles would increase the strength of the bite. The usual condition in the finches is that all of these muscles have increased in size, but that the relative increase of the several muscles differs in the different groups. The descriptions of the jaw muscles will be for the gray jay (Fig. 11), with comparative notes on their structure in the finches.

a) M. adductor mandibulae. This is usually the largest of the jaw muscles or is second in mass only to the M. pterygoideus. Without doubt, it is the most complex of the jaw muscles. The M. adductor mandibulae is the most posterior of the dorsal adductors of the mandible and takes origin from the lateral side of the skull posterior to the orbit, and from the outer rim of the orbit, and inserts on the dorsal edge and lateral side of the mandible. The action of the M. adductor mandibulae is to raise the mandible, but because of the anterior position of its insertion, it is probably most important when the mandible is more than half closed. The anterior position of its insertion gives the M. adductor mandibulae a mechanical advantage through increased leverage (the farther a force is applied from the fulcrum point, which in this case is the quadrate-articular hinge, the greater is the resulting force). The anterior insertion also results in a mechanical disadvantage when the bill is wide open because of the unfavorable angle of insertion — a very acute angle which means that most of the strength of the muscle is lost (see Mollier, 1937; and Dullemeijer, 1951, for a discussion of the "unprofitable" angle of insertion). The M. adductor mandibulae usually does not leave a muscle scar on the roof of the skull in passerine birds, but in several of the heavy-billed finches, such as the evening grosbeak and the cardinal, a slight depression can be seen on the roof of the skull outlining its area of insertion.

b) M. pseudotemporalis superficialis. This tripartite (sometimes bipartite) muscle originates from the posterodorsal wall of the orbit, just medial to the origin of the M. adductor mandibulae, and inserts on the medial side of the mandible close to the quadrate hinge. Its action is to raise the mandible, but in

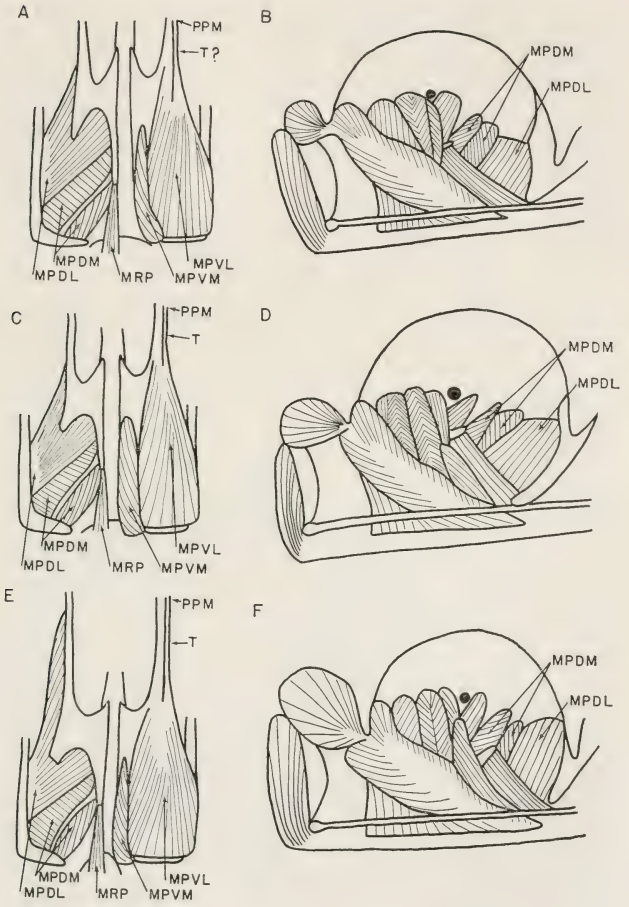

Figure 16. Jaw muscles of: (A and B) *Spizella;* (C and D) *Zonotrichia*; and (E and F) *Pipilo.*

contrast to the M. adductor mandibulae, the M. pseudotemporalis superficialis is probably more important as an adductor of the mandible when the bill is opened widely. Its insertion close to the quadrate hinge allows it to close the bill rapidly at the price of a reduction of the exerted force. It is interesting that in the cardueline finches, the enlarged part of the M. pseudotemporalis superficialis has the most anterior insertion. The large mass and importance of this muscle in the finches is indicated by the several bony processes on the posterodorsal wall of the orbit to which this muscle attaches. These processes are absent in most other passerine birds, especially in the thin-billed insect-eaters.

c) M. pseudotemporalis profundus. This muscle originates from the orbital process of the quadrate and inserts on the medial side of the mandible anterior to its insertion of the M. p. superficialis and opposite the insertion of the M. adductor mandibulae. Like the M. pterygoideus, this muscle has the dual function of raising the lower jaw and depressing the upper jaw; however, it is difficult to determine which of these functions is the most important. The M. pseudotemporalis profundus is a relatively small muscle as compared to the other jaw muscles, especially the other adductors of the mandible. Increase in the mass of this muscle could serve for increased strength of the adductors of the mandible or for increased strength of the palatine retractors (= depressors of the upper jaw). The latter function may be the more important because this muscle is relatively small in the finches. It is also possible that the M. p. profundus functions to oppose the outward forces of the M. adductor mandibulae and to strengthen the quadrate hinge.

d) M. pterygoideus. This muscle is the most anterior of the jaw muscles and lies ventral and anterior to the M. pseudotemporalis profundus. The M. protractor quadrati lies dorsal to the M. pterygoideus and separates it from the M. pseudotemporalis superficialis. The M. pterygoideus has already been described and discussed. I need only to emphasize that the medial parts of the M. pterygoideus — the depressors of the upper jaw — are relatively more highly developed in groups with a highly kinetic upper jaw while the lateral subdivisions are more highly developed in the groups which have only a slightly kinetic upper jaw. In the finches, only the dorsal portions of the M. pterygoideus can be seen through the orbit.

Gross muscle function. The action of a muscle depends not only upon its size and attachment, but upon the orientation of its fibers. In some muscles, the fibers run parallel to one another

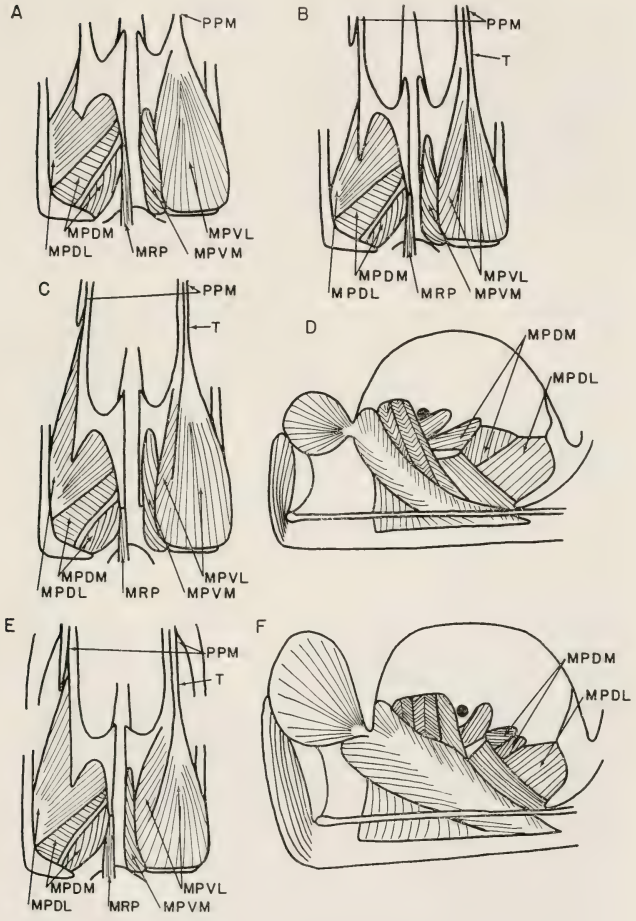

Figure 17. Jaw muscles of: (A) *Melospiza*; (B) *Piranga*; (C and D) *Passerina*; and (E and F) *Cardinalis*.

and to the longitudinal axis of the muscle, while in others, the fibers are oblique to the longitudinal axis and insert on a tendon or an aponeurosis. The former are usually called parallel-fibered or simple muscles, and the latter, pinnate or complex muscles. Pinnate muscles are not identical in their internal structure, but vary greatly in the number of central tendons and in the directions of their fibers. The action of parallel-fibered muscles is relatively easy to analyze. Since all of the muscle fibers are oriented along the longitudinal axis of the muscle, the speed, strength and distance of the muscle contraction is proportional to the number of fibers that have contracted. The angle of insertion of the muscle fibers on the central tendon and the change in this angle during contraction must be considered in addition to these factors when one analyzes the action of a pinnate muscle. Few workers have considered pinnate muscles in detail with the result that virtually nothing is known about their action. Pfuhl (1936) is the only worker, to my knowledge, who has attempted to analyze pinnate muscles with the use of trigonometrical models. The reader is referred to his paper and those by Mollier (1937) and Dullemeijer (1951).

Both parallel-fibered and pinnate muscles are found in the jaw muscles of passerine birds; indeed, some of the jaw muscles, such as the M. adductor mandibulae, are among the most complex muscles found in birds. The same muscle may be parallel-fibered in some species and pinnate in others. Some workers, notably Beecher, have differentiated between parallel-fibered and pinnate muscles in their functional discussions. But their basic assumptions are so simplified that their results are misleading. In general, they have assumed that pinnate muscles are one type and parallel-fibered muscles are another, that pinnate muscles are universally more efficient (i.e., stronger) than parallel-fibered muscles and that pinnate muscles have evolved only in response to a selection force for increased strength. In an attempt to clarify some of these problems, I have started an analysis of the action of pinnate muscles using trigonometrical models and hope to present the results in the near future. A few tentative conclusions will, however, be outlined to illustrate the major aspects in the action of pinnate muscles.

The angle of insertion of the muscle fibers on the central tendon determines the relative number of fibers, the relative amount of useful force and the relative speed of central tendon. If pinnate muscles of equal lengths and diameters are compared, the number of fibers increases, the amount of useful force decreases

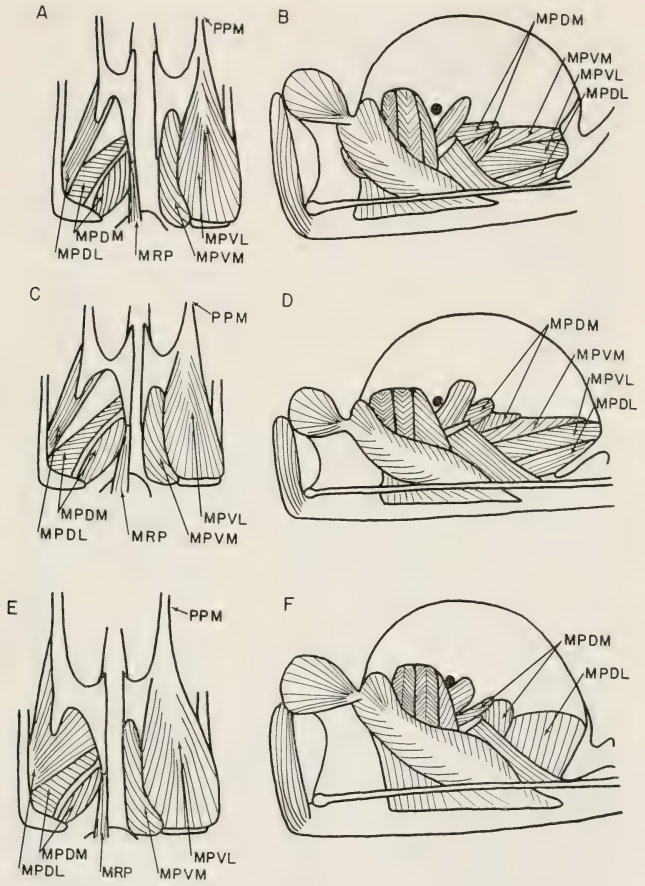

Figure 18. Jaw muscles of: (A and B) *Vireo*; (C and D) *Seiurus*; and (E and F) *Molothrus*.

and the relative speed increases as the angle of insertion of the fibers increases. Similarly, during contraction, the angle of insertion increases with a corresponding decrease in the amount of useful force and an increase in speed. Thus it can be seen that pinnate muscles can be not only strong muscles acting over a short distance, but also weak, rapid muscles acting over a long distance. For example, the M. pseudotemporalis superficialis is frequently pinnate. This muscle inserts on the mandible close to the quadrate hinge; hence it serves to raise the mandible rapidly, but with little force. Most likely, it has become pinnate in response to a selection force for increased speed. On the other hand, the M. adductor mandibulae is a "power muscle." It inserts on the mandible far anterior of the quadrate hinge and serves to raise the mandible with great force. Also, its action is frequently over a very short distance as, for example, when a finch cracks a seed. Thus, this muscle has become pinnate in response to a selection force for increased strength.

Unless complex pinnate muscles, such as the jaw muscles, are dissected in great detail and all possible reasons for their becoming pinnate are considered, it is better to omit this factor from consideration. For this reason, I have not attempted to compare the pinnateness of the several jaw muscles in the finches. But it is obvious that the degree of pinnateness cannot be omitted if we hope to understand the function of the jaw muscles and to compare properly the jaw muscles of different groups of passerine birds. Thus, in investigations of the jaw muscles, there is really no choice but to dissect the pinnate muscles in great detail and to take great care in interpreting their functional significance.

Relationship between the processes of the skull. Another factor influencing the strength of the bite, but quite apart from the muscles themselves, is the size, shape, and spatial relationships of the various bony processes to which the muscles attach. Changes in these processes would modify the leverage of the jaw muscles. The role of leverage in the action of the jaw muscles has been studied extensively by Kripp (1935) and more recently by Fisher (1955). However, most workers completely overlook the importance of the bony processes in the action of the jaw muscles. A notable exception is Beecher's discussion (1951a, p. 420) of the orbital process of the quadrate. He shows this process to be a lever and discusses the functional significance of the difference in its length in two genera of blackbirds.

The variation in several bony processes of the skull is directly correlated with changes in the jaw muscles. Some examples are

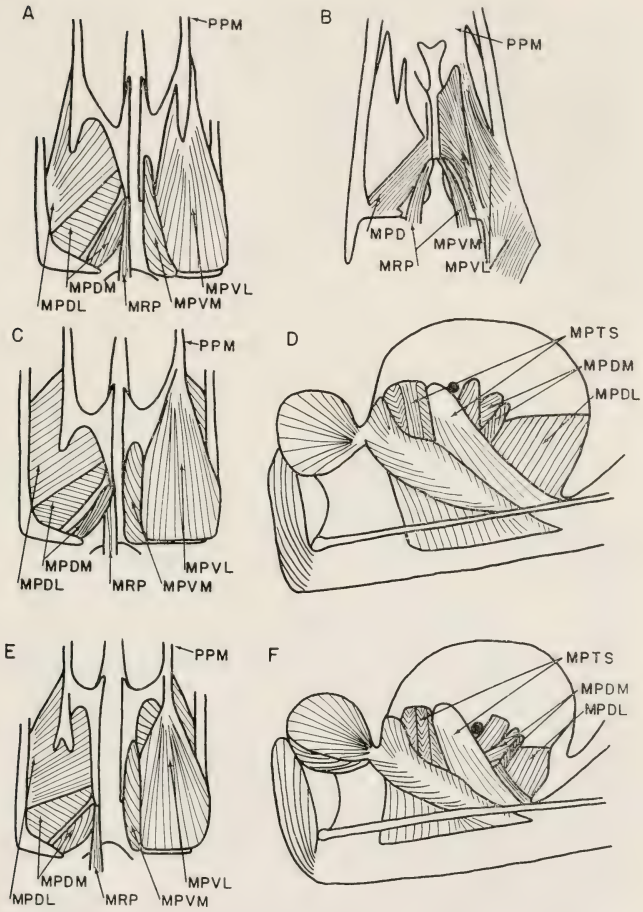

Figure 19. Jaw muscles of: (A) *Quiscalus;* (B) *Dacnis* (redrawn from Moller, 1931); (C and D) *Fringilla*; and (E and F) *Spinus.*

the size of the medial process of the mandible, the length of the transpalatine process (and hence the distance between this bone and the mandible), the length of the palatines themselves, the size of the auditory bullae ("inflated squamosal region" Tordoff, 1954a, pp. 9-10, which is associated with the mass and length of the M. depressor mandibulae), and finally, the free palatine process of the premaxilla as seen in the cardinals. This list could be easily expanded, but it is sufficient to show that a comparative study of the musculature of so complex a system as the jaw muscles must include the detailed mechanics of the underlying bone-lever system. The converse is also true; a study of the skull must also include the muscles and other influencing factors.

Comparison of the jaw muscles in the finches. The jaw muscles of the "nine-primaried" and "ploceid" finches will now be compared, using the information presented in the preceding sections. The major question to be answered is: Has the same morphological adaptation for cracking seeds evolved in the several groups of finches, or have different adaptations evolved in these groups (cf. multiple pathways of evolution)? This question may appear to be unrelated to the central problem of this paper — the evolution of the palatine process of the premaxilla — especially when the jaw musculature of the finches is compared, but it is essential to study the entire set of jaw muscles before the differences in the M. pterygoideus can be understood and its correlation with the palatine process of the premaxilla clarified. In addition to comparing the jaw muscles of the several groups of finches, I shall compare, whenever possible, a small-billed species with a large-billed species of the same group, to determine whether there is any variation in the jaw muscles within familes or subfamilies of passerine birds and more precisely, whether the jaw muscles have changed within a group of finches to meet the demands of a stronger bite. I shall describe the small-billed species first and then compare it to the large-billed species. This procedure is used for convenience only and not to imply that the small-billed species is primitive in the group or that evolution in the finches has always been from the small- to the large-billed size.

The jaw muscles of a warbler (*Seiurus aurocapillus*, Figs. 18C and 18D) and a vireo (*Vireo olivaceus*, Figs. 18A and 18B) — both insect-eaters with thin bills — and included, in addition to those of the gray jay, for comparison with the heavy-billed seed-eaters. These species were chosen because of convenience only and not because of any special relationship to the finch groups

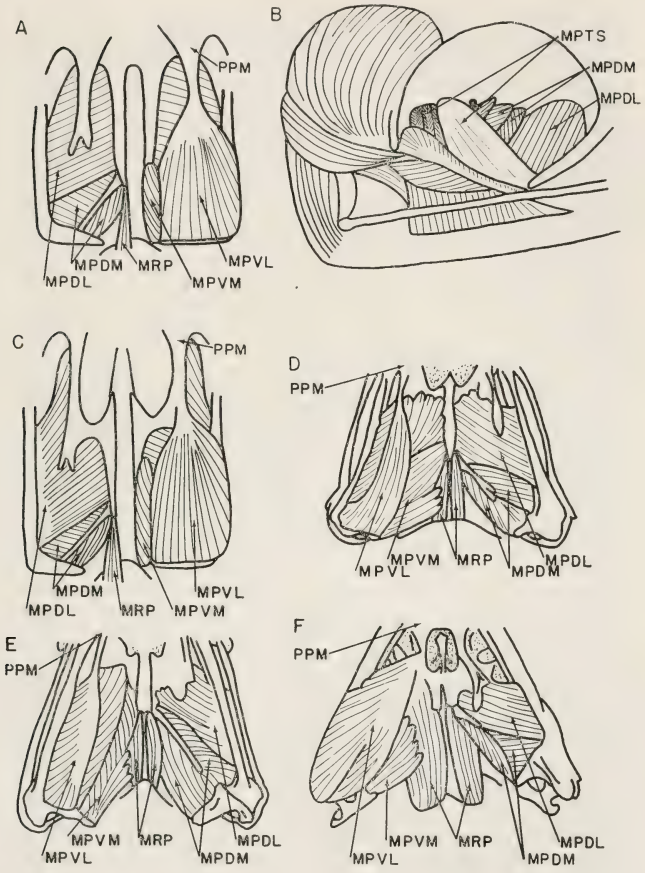

Figure 20. Jaw muscles of: (A and B) *Hesperiphona;* (C) *Carpodacus;* (D) *Carduelis* (redrawn from Fiedler, 1951); (E) *Pinicola* (redrawn from Fiedler, 1951); and (F) *Loxia* (redrawn from Fiedler, 1951).

discussed here. When examining the jaw muscles of these insectivorous birds, the general impression one receives is that the muscles are weakly developed, or, to put it in another way, the muscles are not overly developed and do not show any specializations for a strong bite. For example, the origin of the M. adductor mandibulae has not spread over the roof of the skull and the M. pseudotemporalis superficialis has not expanded to cover the M. p. profundus. One of the most striking features in the jaw muscles of these species is the relative weakness of the parts of the M. pterygoideus that adduct the mandible, especially the M. p. dorsalis lateralis. In the warbler and the vireo, parts of the M. p. ventralis may be seen between the two halves of the M. p. dorsalis when the jaw muscles are viewed through the orbit — an indication of the weakness of the M. p. dorsalis lateralis. This muscle is large in the gray jay.

The emberizine finches. The emberizine finches may be considered as generalized or, better, as unspecialized seed-eating birds; they feed on smaller seeds and are more insectivorous than most other groups of finches. In accordance with these feeding habits, the morphological specializations for seed-eating are less developed than in other finches. For example, the bill of the emberizines, although shorter and stouter than the bill of insectivorous birds, is longer and thinner than the bill of other groups of finches. The palatine process of the premaxilla is essentially the same as in the insect-eaters; it lies along the prepalatine process and is more or less fused with that bone. The major exceptions are *Melopyrrha* and *Tiaris,* which have a free palatine process such as is found in the cardinals, and *Oryzoborus,* which has a lateral flange on the prepalatine process similar to that found in the cardueline finches. These "aberrant" genera will be discussed in the section on relationships. The emberizine finches are a useful starting point, for their lack of extreme specializations in the skull and in the jaw muscles allows us to analyze the basic modifications in these structures for seed-cracking. Insectivorous and granivorous birds are not sharply distinct types, but grade into one another; hence, it is not always possible to distinguish insectivorous from granivorous adaptations.

The jaw muscles of a field sparrow (*Spizella pusilla,* Figs. 16A and 16B) are similar to those of the warbler and the vireo except for the increase in mass of the mandible adductors. The M. adductor mandibulae and the M. pseudotemporalis superficialis are larger and more pinnate than those in the warbler, but they

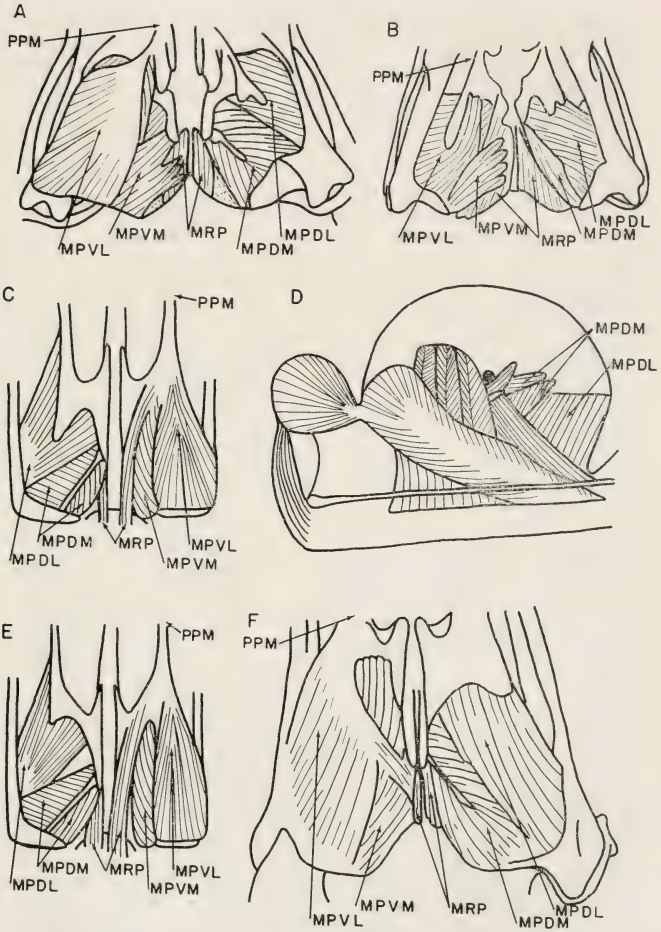

Figure 21. Jaw muscles of: (A) *Coccothraustes* (redrawn from Fiedler, 1951); (B) *Lonchura* (redrawn from Fiedler, 1951); (C and D) *Passer*; (E) *Sturnus*; and (F) *Corvus* (redrawn from Fiedler, 1951).

are quite similar in other respects. The M. pseudotemporalis profundus is not hidden by the M. p. superficialis as in the carduelline finches. Most striking is the expansion of the M. pterygoideus dorsalis lateralis which completely covers the ventral parts of the M. pterygoideus. Turning to the ventral aspect of the M. pterygoideus, the increase of the mandible adductors at the expense of the palate retractors can be readily seen. Yet the palate retractors are still relatively large. A tendon of the M. pterygoideus ventralis lateralis appears to extend forward along the palatine to the position of the semifused palatine process of the premaxilla. I have shown this tendon running forward in my drawing of the field sparrow (Fig. 16B), but wish to emphasize that it is not certain whether this tendon really exists. The small size of the field sparrow makes it difficult to determine whether the strip of connective tissue seen along the prepalatine process is the periosteum of that bone or a tendon of the M. pterygoideus. This problem may be resolved by histological examination, but I am not sure whether it can ever be decided beyond all doubt. Therefore, although there is an indication in the field sparrow of a direct association between the M. pterygoideus and the palatine process by means of a tendon, this must still be proven.

In such a medium-billed species as the white-throated sparrow (*Zonotrichia albicollis*, Figs. 16C and 16D) and the larger rufous-sided towhee (*Pipilo erythrophthalmus*, Figs. 16E and 16F), the jaw muscles increase in mass as the size of the bill increases. In the towhee, there is a muscle scar on the roof of the skull outlining the origin of the M. adductor mandibulae, a reflection of the increase in size of this muscle. The most conspicuous changes in the muscles are, however, the increase in size of the anteromedial part of the M. pseudotemporalis superficialis toward the carduelline condition and the increase in the adductor parts of the M. pterygoideus. Both the M. p. dorsalis lateralis and the M. p. ventralis lateralis increased in mass. The change in the M. p. v. lateralis is of particular interest. The lateralmost fibers of this muscle converge on a tendon that runs along the lateral edge of the palatine up to the fused palatine process of the premaxilla. Although this tendon is easily destroyed during dissection, it can readily be demonstrated in the towhee. The tendon is intimately associated with the periosteum of the palatine. In the smaller species, even if it is present, the tendon is almost indistinguishable from the periosteum of the palatine, as for example in the field sparrow. The towhee, the largest of these

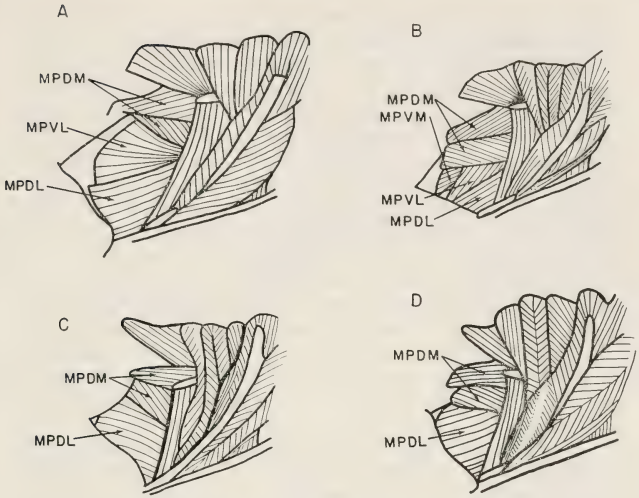

Figure 22. Jaw muscles as seen through the orbit of: (A) *Phylloscopus*; (B) *Oporornis*; (C) *Melospiza*; and (D) *Molothrus* (redrawn from Beecher, 1953). The M. pterygoideus has been labeled according to my identification. Beecher's identifications for *Phylloscopus* are: M. pterygoideus dorsalis anterior (3a) = MPDM (anterior half); M. p. dorsalis posterior (3b) = MPDM (posterior half); M. p. ventralis anterior (4a) = MPDL; M. p. ventralis posterior (4b) = MPVL (usually, but sometimes part or all of the MPVM is included in this muscle by Beecher).

species, has a well-developed tendon very similar to the tendon of the M. p. ventralis lateralis that attaches to the free palatine process of the premaxilla in the tanagers and the cardinals. Thus, with increase in the size of the bill in these species of emberizine finches, the M. pseudotemporalis superficialis changes toward the cardueline condition while the M. pterygoideus changes toward the cardinal condition.

Not all emberizine finches show these changes in the structure of the jaw muscles. The fox sparrow (*Passerella iliaca*, Figs. 15E and 15F), another heavy-billed species, tends toward the cardueline condition not only in the structure of its M. pseudotemporalis superficialis, but also in the structure of its M. pterygoideus ventralis lateralis. The lateralmost fibers of this latter muscle do not send a long tendon forward along the palatine, but rather insert on the distal tip of the transpalatine process by means of

a short tendon. In accordance with this condition of the M. p. v. lateralis, the tip of the transpalatine process is forked in a manner similar to that seen in the cardueline finches. The lateral branch of the transpalatine process is associated with the fibers inserting on the medial side of the mandible while the medial branch is associated with the fibers inserting on the medial process of the mandible. Thus, the changes in the structure of the jaw muscles in the fox sparrow are exclusively toward the cardueline condition. I have dissected a specimen of the Lincoln sparrow (*Melospiza lincolnii*) and a specimen of the song sparrow (*Melospiza melodea,* Fig. 17A). These species are smaller than the fox sparrow and consequently have smaller (both absolute and relative) jaw muscles. Nevertheless, the structure of their M. pseudotemporalis and their M. pterygoideus ventralis lateralis is similar to those seen in the fox sparrow. It is, however, not certain whether these species lack the lateral tendon as seen in the fox sparrow, or have the tendon which was overlooked because of the small size of these species.

In the emberizine finches, all of the adductor muscles of the mandible and the retractors of the palate have increased in size. This increase is relatively "even" in that one adductor or retractor has not assumed a highly dominant role in closing the bill. Sims (1955, p. 382) points out that the "division of labor" between the several muscles which close the bill has two important attributes. First, it spreads the origin of these muscles and hence the strain on the bones over a larger area of the skull. Second, the "harmful" components of force are counteracted. For example, the M. adductor mandibulae tends to pull the mandible backwards and outwards as well as upwards. These backward and outward forces are counteracted by the M. pterygoideus which pulls the mandible inward and forward as well as upward and by the M. pseudotemporalis superficialis and the M. p. profundus, both of which have inward and backward components as well as upward components of force. If only one of these adductors were powerfully developed, as for example, the M. adductor mandibulae, it might put uneven forces on the mandible and possibly might even disarticulate it during a particularly powerful contraction. This would, however, never happen because the jaw muscles function and evolve as a unit. Consider, for example, a bird which is becoming a seed-eater and thus subject to a selection force for a larger bill and stronger jaw muscles. As soon as one adductor begins to become disproportionally large, it would put an uneven strain on the mandible.

The other adductors must enlarge to counteract its "harmful" components of force or the bird will have a selective disadvantage. If the other adductors did not enlarge, the bird would be selected against long before the one muscle became large enough to disarticulate the mandible.

Compared to a warbler or a vireo skull, the skull of an emberizine finch is a more substantial structure with a shorter and heavier bill and a stouter palate. Yet, it cannot be called a reinforced skull, for the interorbital septum and the anterior part of the interpalatine space are both unossified. Nevertheless, there are other skeletal adaptations for seed-eating, such as the bony processes on the posterior wall of the orbit and on the lateral side of the skull, which are directly correlated with the increase in the mass of the adductor muscles, but these do not need to be considered separately. One of the most important features of the skull is the fact that the upper jaw has retained its kinetic property, which plays a large role in the seed-cracking method of the emberizines.

In the emberizines, a seed to be cracked is held between the jaws just anterior to the angle of the mandible. This is approximately the point where the palatine meets the premaxilla, where the nasal process of the maxilla meets the body of the maxilla, and where the horny covering of the upper jaw ends. This point is just anterior to the insertions of the adductor muscles — hence as close as possible to the jaw articulation and the point where the maximum force may be exerted on the seed — and yet it is still the most reinforced part of the skull. When the adductor and retractor muscles contract, the upper jaw is depressed and the lower jaw is raised until the seed coat is cracked. This pincer action can be compared to the cracking of the shell of a nut by means of a nutcracker or a pair of pliers. The chief advantage of the "nutcracker" method is that the initial shocks are borne by the jaws which form a system partially isolated from the braincase. This system permits the retention of a lighter skull and eliminates the need for reinforcement of the braincase. A light skull has a lower inertia which means that smaller muscles are needed to move it — a distinct advantage for a flying animal. Such a light skull and a faster-closing bill enables the emberizine finches to capture insects, but also limits them to smaller seeds.

The cardinaline finches. The cardinaline finches feed, as a rule, more exclusively on seeds and perhaps on larger seeds than do the emberizine finches; therefore, it is not surprising that they

possess more specialized modifications for seed-eating. They have a shorter and more conical bill with a more decurved upper jaw and a greater angle in their mandible than the emberizines. The most conspicuous specialization, however, is the palatine process of the premaxilla, which lies free of the palatine and is situated in the space between the palate and the jugal bar. The other osteological features of the cardinaline skull will be described below.

The jaw muscles of the indigo bunting (*Passerina cyanea*, Figs. 17C and 17D), when viewed through the orbit, are very similar to those of the field sparrow. The M. adductor mandibulae has expanded over a larger area of the roof of the skull, but otherwise the differences between these species appear to be minor ones of proportions. However, the M. pterygoideus of the indigo bunting, when viewed from beneath, is unlike that seen in the field sparrow. The superficial fibers on the lateral half of the M. p. ventralis lateralis form a distinct bundle that originates from the free palatine process of the premaxilla by means of a separate tendon. These fibers and tendon would correspond to the lateral fibers and tendon seen in the towhee. Examination of the rest of the M. pterygoideus shows that the palatine retractors are still well developed.

The cardinal (*Cardinalis cardinalis*, Figs. 17E and 17F) is one of the largest-billed members of this group. Most of its jaw muscles, as seen through the orbit, are similar to those of the indigo bunting except for the M. adductor mandibulae, which has become larger and has spread over the roof of the skull. In fact, this muscle leaves a clearly visible muscle scar outlining its area of origin on the roof of the skull. The M. pterygoideus, especially its lateral subdivisions, has also enlarged greatly. Again, the lateral and superficial part of the M. p. ventralis lateralis originates by means of a tendon from the palatine process of the premaxilla. These fibers comprise less than 5 per cent of the total mass of the M. pterygoideus, not 25 per cent as Tordoff estimates. The functional significance of this separate bundle of fibers will be discussed later. It is interesting to note that there has been no expansion of the medial part of the M. pseudotemporalis superficialis in the cardinals. Possibly, the genetic capacity for this structure had never appeared in the cardinals or perhaps this muscle cannot function in harmony with the superficial bundle of the M. p. ventralis lateralis.

The fact that the cardinals feed more exclusively on seeds is reflected in the structure of their skull as well as in the jaw

muscles. The bill is shorter and broader, and the bones of the palate are stouter than those in the emberizine finches. The entire skull is reinforced; the nasal septum and the anterior interpalatine space are ossified, the maxillo-palatines are fused to the vomer and the nasal process of the maxilla is at right angles to the body of the mandible and parallel to the force on the upper jaw. Yet, the upper jaw has retained its kinetic property — a fact that is reflected in the fusion between the vomer and the maxillo-palatines and in the medial ossification at the jugal-maxilla connection, both of which are absent in the cardueline finches.

The cardinals crack seeds by the nutcracker method as has just been described for the emberizines; the mobility of the upper jaw permits the use of this method. Thus the cardinals do not need heavy bosses on the upper jaw to protect the braincase. The function of the separate bundle of fibers of the M. p. ventralis lateralis is still a problem. Obviously it serves some particular function, for its structure is relatively constant within the cardinals — an indication that a selection force responsible for its maintenance is present. These fibers do not appear to play a vital part in cracking seeds; the other adductors of the mandible and retractors of the palate are many times more massive than this bundle of fibers and are probably able to crack seeds without any aid from these superficial fibers of the M. p. ventralis lateralis. Because of their greater length and their insertion on the mandible near its articulation and on the ventral rim of the medial process of the mandible, these fibers appear to have as their chief action, the raising of the mandible. These fibers would raise the mandible rapidly because of their insertion on the medial process as has been discussed above (p. 392). I suggest, therefore, that the function of the superficial fibers of the M. p. ventralis lateralis is to raise the mandible quickly until the seed or insect is grasped firmly between the jaws. The more massive adductors and retractors would then take over the task of cracking the seed. If this assumption is correct, the origin of the separate bundle of fibers and the free palatine process is a mystery. It does not appear to be an essential modification for seed-eating; indeed, it is somewhat contrary to what would be expected. Perhaps it is a specialization for a fast-closing bill to allow the cardinals to feed on insects as well as on seeds, or perhaps it is a modification of a similar specialization in the insectivorous ancestors of the cardinals (possibly the tanagers?).

The cardueline finches. The carduelines differ from the emberizines and agree with the cardinalines in feeding more on seeds (in fact, the carduelines feed almost exclusively on seeds), and in having a shorter, conical bill with a decurved upper jaw and a greater angle in the mandible. The chaffinch and brambling (*Fringilla*) are exceptions and resemble the emberizines in the structure of their skulls. The similarity between the cardinals and the carduelines is a superficial one, for these groups are strikingly different in the structure of the skull and in the arrangement of the jaw muscles. For example, in the cardueline finches, the palatine process of the premaxilla is completely fused with the palatine, and in its stead is a lateral flange as described above. Again *Fringilla* differs from the rest of the cardueline finches in having an unfused palatine process in the adult and in lacking completely the lateral flange.

The jaw muscles of the goldfinch (*Spinus tristis*, Figs. 19E and 19F), as seen through the orbit, are quite different from those in the emberizine finches or the cardinals. The M. adductor mandibulae is relatively large for a bird the size of a goldfinch, with the portion spread over the roof of the skull doubled — a condition not seen in any other passerine family examined in this study. The M. pseudotemporalis superficialis has enlarged unevenly. Only the anteromedial part of this muscle has enlarged to a great degree; the lateral parts of the M. p. superficialis appear as a small isolated muscle sandwiched between the larger medial portion and the M. adductor mandibulae. The large medial portion of the M. p. superficialis almost completely covers the M. p. profundus. Those muscles associated with the raising and lowering of the upper jaw, the M. p. profundus and the M. protractor quadrati, are relatively small muscles with fleshy origins and insertions. Turning to the ventral side of the head, the large M. pterygoideus can be seen. Again, the mandible adductor parts of this muscle have enlarged while the palatine retractors have decreased in size. Special note should be taken of the M. p. ventralis lateralis. It takes origin only from the transpalatine process; no muscle fibers or tendons run forward to attach to the palatine in the region of the lateral flange. As in the fox sparrow, the tip of the transpalatine process is forked; the lateral branch is associated with the fibers running to the ramus of the mandible while the medial fork is associated with those fibers running backwards to the medial process of the mandible.

If the jaw muscles of a medium-billed species, such as the purple finch (*Carpodacus purpureus,* Fig. 20C), and those of a large-billed species such as the evening grosbeak (*Hesperiphona vespertina,* Figs. 20A and 20B), are examined, two important changes from the goldfinch condition are discernible. First, the M. adductor mandibulae has increased in size until, in the evening grosbeak, its origin spreads over most of the roof of the skull and leaves a well defined muscle scar. Second, the medial part of the M. pseudotemporalis superficialis has increased in mass to dominate the muscles inside the orbit. It completely obscures the M. p. profundus and almost completely hides the M. protractor quadrati and the lateral part of the M. pseudotemporalis superficialis. The two major dorsal adductors of the mandible — the M. adductor mandibulae and the medial part of the M. pseudotemporalis superficialis — converge upon the mandible from the outside and the inside respectively — an excellent example of two muscles so placed that their "harmful" effects are counteracted. There are no significant changes other than increase in mass in the structure of the M. pterygoideus.

Sims (1955) has reported on the jaw muscles of the hawfinch (*Coccothraustes coccothraustes*), a species very similar and apparently closely related to the evening grosbeak. Unfortunately, his excellent analysis of the skull and the jaw muscles is marred by several misidentifications, such as the M. quadrato-mandibularis in his figure 4B (this is actually the enlarged medial part of the M. pseudotemporalis superficialis) and the M. p. ventralis lateralis anterioris in his figure 5B (this is probably the M. p. dorsalis lateralis).

I was fortunate in being able to examine two specimens of the chaffinch (*Fringilla coelebs,* Figs. 19C and 19D). In most respects, the jaw muscles are similar to those of the least specialized cardueline finches, although they are not as powerful. The most significant feature of the dorsal adductors is the enlarged medial portion of the M. pseudotemporalis superficialis. This muscle is identical to that in the heavier-billed cardueline finches and, in fact, it completely covers the M. p. profundus, as in the evening grosbeak. The M. adductor mandibulae is larger than expected; its origin has expanded over as large an area of the roof of the skull as in the larger towhee. However, the M. adductor mandibulae of the chaffinch is not as specialized as in the carduelines, but is similar to that seen in the emberizine finches (see Fiedler, 1951, pp. 241-242). Turning to the ventral aspect of the M. pterygoideus, we find that it is almost identical

to that seen in the goldfinch, the main difference being that the chaffinch has a less massive muscle. The unfused palatine process of the premaxilla was clearly visible, but there was no connection between it and the M. p. ventralis lateralis; in fact, the M. pterygoideus of the chaffinch is very reminiscent of that seen in the fox sparrow.

The cardueline finches (with the exception of *Fringilla,* Eber, 1956) feed almost exclusively on seeds and hence have a massive reinforced skull, one that is even heavier than the cardinaline skull. The interorbital septum, the nasal septum, and the interpalatine space are more heavily ossified in the carduelines than in the cardinals. The most conspicuous difference between the two groups is the lack of a free palatine process and the development of a lateral flange on the prepalatine process with an overlying horny pad of rhamphotheca in the cardueline finches. The upper jaw has lost most of its mobility, but the fact that it is not rigidly fused to the cranium as stated by Sims (1955, p. 373) could be ascertained by boiling skulls of *Hesperiphona* and *Coccothraustes* for a minute or two as suggested by Beecher (1951a, p. 412). This technique softens the dried ligaments and restores flexibility to the skull. However, Sims' conclusion is still correct, for the upper jaw is essentially stationary during the closing of the bill. The immobile upper jaw plus the presence of the heavy bosses of bone and rhamphotheca suggest that the cardueline finches employ a method other than that of a nutcracker to crack the seed shell.

A seed to be cracked by a cardueline finch is placed in the corner of the mouth, just anterior to the angle of the mandible. The seed lies between the heavy pads of the upper jaw and those of the lower jaw and is held in place by the tongue, as shown by Eber (1956). Upon contraction of the adductor muscles, the mandible is raised and forced against the seed until its shell cracks. In this way, the apparatus resembles the action of a vise. Since the upper jaw is continuous with the braincase, the cracking shock must be transmitted across the skull without harm to it or to the contained organs. The heavy bosses on the upper jaw provide an even distribution of the shock, protecting the braincase and the brain from injury. Perhaps the slight amount of mobility of the upper jaw may partly absorb the shock wave that accompanies the actual cracking of the seed. The heavy pads of rhamphotheca may serve to absorb some of the shock wave, but this is open to question. The vise method is intrinsically

no more efficient than the nutcracker method, but a heavier seed can be cracked with the vise method since the bony elements involved are inherently larger. Not only the palatine complex, but the entire skull is used to transmit the forces and shocks of seed-cracking; hence larger forces are possible for an equal amount of stress on the bone. Sims has shown that the hawfinch must exert a force of 100 to 150 pounds when it cracks an olive stone. However, the powerful vise system is developed at the expense of the mobility of the upper jaw which limits the carduelline finches to a rather exclusive diet of seeds (Eber, 1956). The "slender-billed" chaffinch does not have such a specialized bill and feeds extensively on insects during the summer. It probably uses the "nutcracker" method of cracking seeds rather than the "vise" method.

The above descriptions of the nutcracker and the vise methods of seed-cracking, being based completely upon deductive reasoning from the structure of the skull and the jaw muscles in several groups of finches, have raised more problems than they have solved. First, direct observations or experiments are needed to verify my conclusions as to function and to establish the exact morphological and functional differences between the two methods. It must be emphasized that the important functional difference between the nutcracker and the vise methods of cracking seeds is not in terms of applying force on the seed, but in terms of protecting the braincase from the shocks associated with the breaking of the seed coat. In the nutcracker method, these shocks are isolated within the jaw apparatus, while in the vise method, these shocks are distributed evenly to the braincase by the heavy bosses of bone and rhamphotheca and thus are prevented from concentrating on one bony element. The method used in each group of finches and the degree of specialization in each group must be determined. The difference between the extreme types, such as the cardinals and the carduelines, is clear, but that between the less specialized forms is quite fuzzy. For example, the emberizine finches are best classified as having a "primitive" nutcracker method of seed-cracking. Where is the boundary between the primitive nutcracker method and the specialized nutcracker or the vise methods, both of which are presumed to have evolved from the emberizine condition? I have assumed for the purposes of this paper that the presence of a lateral flange indicates that the vise method is used. Therefore, the estrildids, the advanced ploceids, *Oryzoborus* of the

Emberizinae and *Psittirostra* of the drepaniids would use the vise method of seed-cracking; however, there is no available evidence supporting a correlation between the lateral flange and the vise method. These problems must be solved before we can obtain a complete picture of the evolution of seed-eating in the passerines and of the origin of the several finch-like groups.

Other finches. The jaw muscles of three other seed-eating passerines, the horned lark (*Eremophila alpestris,* Figs. 12C and 12D), the cowbird (*Molothrus ater,* Figs. 18E and 18F), and the house sparrow (*Passer domesticus,* Figs. 21C and 21D) were dissected. Although seeds comprise a large part of the diet of these species, their jaw muscles are relatively unspecialized when compared to those of the cardinaline and the carduelinc finches. The jaw muscles of the house sparrow and the cowbird are similar to one another and to those found in the smaller emberizine finches and show the usual development of the adductor muscles. Neither species has any specialization of the M. pseudotemporalis superficialis or the M. pterygoideus; both have an expansion of the M. adductor mandibulae over the side of the skull to about the same extent as in the towhee. The medial part of the M. adductor mandibulae is expanded in both species and bulges inward to cover part of the M. pseudotemporalis profundus. This slip of the M. adductor mandibulae has not become specialized in either species. The upper jaws of the house sparrow and of the cowbird are kinetic, suggesting that these birds probably use the nutcracker method of seed-cracking. In almost all respects, both species are comparable to the emberizine finches in the specialization of their seed-cracking modifications.

The jaw muscles of the horned lark are the most interesting because they have evolved a quite unique specialization (for seed-cracking ?) not found in any other species of passerine birds I have examined. The M. adductor mandibulae has not spread over the side of the skull roof as in other seed-eating birds. Instead, the medial part of this muscle has enlarged and become pinnate. This large medial slip of the M. adductor mandibulae may be able to provide much of the force needed for cracking seeds that is usually supplied by the lateral parts of this muscle and by the M. pterygoideus, both of which are poorly developed in this species. It is also conceivable that this pinnate slip has a special function that is totally independent of seed-cracking. Larks (all species ?) swallow seeds whole and thus would not need strong jaw muscles. More work correlating the feeding

methods with the jaw muscles of the larks is needed before this problem is solved.

Résumé on the feeding methods in the finches. A brief review of the methods of seed-cracking in the three groups of "nine-primaried finches" and the associated adaptations may now be given. The emberizine sparrows (plus the house sparrow and the cowbird) can be regarded as "generalized" seed-eaters, lacking the extreme specializations for seed-cracking. The adductors of the mandible and the retractors of the palate are equally well developed, and the upper jaw has not lost its kinetic property — the result is the nutcracker method of seed-cracking. Some of the larger-billed emberizines (e.g., the towhee) tend toward the cardinals in their jaw muscles, especially in the structure of the M. pterygoideus; others (e.g., the fox sparrow) tend toward the carduelinе finches. The cardinals are heavy-billed forms that have retained the nutcracker method; hence the skull is still relatively light. Increase in the mass of the M. pterygoideus ventralis lateralis and its lateral tendon has resulted in the free palatine process of the premaxilla. The free palatine process and the movable upper jaw probably preclude the development of the lateral flanges on the prepalatines as seen in the carduelinе finches. The second group of heavy-billed finches — the carduelines — employ another method of cracking seeds, the vise method. However, a presumed "primitive" genus, *Fringilla*, is quite similar to the fox sparrow in the structure of its jaw muscles and probably uses the nutcracker method. In the specialized carduelines, the upper jaw has lost its mobility; it is a nearly stationary block against which the mandible presses. Heavy bosses of bone (the lateral flanges) and rhamphotheca distribute the shocks associated with the cracking of the seed evenly to all parts of the braincase. Only the adductor muscles are well developed in the carduelinе finches; in fact, the muscles associated only with the movement of the upper jaw have become small and are on the verge of becoming functionless.

Conclusions. The primary function of the palatine process of the premaxilla is to provide a point of anchorage for the palatines and hence promote a stronger connection between the palate and the upper jaw. Secondary functions have been superimposed on this primary function in several groups of passerine birds, but these secondary functions do not conflict with the operation of the primary function. The secondary functions have been responsible for the modifications of the palatine process — the development of the free process and the lateral flanges — within

the passerines. Using the data assembled in the preceding pages, I wish to return to the three problems associated with the modifications of the palatine process which have been listed in the beginning of the section on "modifications."

a) Development of the free palatine process: In most groups of passerine birds, there is no connection, either morphologically or functionally, between the M. pterygoideus and the palatine process of the premaxilla. Only in a few groups, such as the cardinals and the tanagers, does part of the M. p. ventralis lateralis take origin from the palatine process. These groups have a free palatine process. Therefore, it may be concluded that the free palatine process as seen in the cardinals serves as the point of origin for the lateral superficial bundle of the M. p. ventralis lateralis. This modification is probably not a specialization for seed-eating as commonly believed, but for rapid rising of the mandible during the early phases of closing the bill, which appears to be a specialization for catching insects.

b) Development of the lateral flange: In a few groups, lateral flanges have developed at the site of the fused palatine processes. These birds have acquired a powerful set of jaw muscles for seed-cracking, but have lost the mobility of the upper jaw. They employ the vise method of cracking seeds in which the seed is cracked by raising the mandible against the stationary upper jaw. The lateral flange plus the overlying pads of rhamphotheca serve to distribute the shock wave (associated with cracking the seed) evenly to all parts of the upper jaw and the braincase.

c) Variation in the degree of fusion between the palatine process and the palatine: Much variation exists in the degree of fusion between the palatine process of the premaxilla and the palatine and in the development and final degeneration of the isolated splint of bone (= the posterior end of the palatine process), such as seen in the emberizine finches. No sharp break exists between a slightly fused palatine process and a free process, or between a heavily and a completely fused palatine process. Tordoff claimed that the functional basis for this variation in fusion from a free process to a completely fused process is the decrease in size of the M. pterygoideus, starting from the cardinal condition. However, in most passerine birds, there is no morphological connection between these two structures; those groups in which part of the M. pterygoideus originates from the palatine process have been discussed above. In the emberizine finches, a tendon from the lateral fibers of the M. pterygoideus originates on or near the palatine process, but there is not the

simple correlation between the size of this muscle and the fusion of the palatine process as claimed by Tordoff. In fact, the palatine process of the towhee is usually completely fused although this species has a larger lateral tendon of the M. pterygoideus than in all other emberizines studied. Therefore, it can be concluded that the variation in the M. pterygoideus is not responsible for the variation in the amount of fusion between the palatine process and the palatine.

This variation in the degree of fusion is the result of two quite different factors. Part is doubtlessly the result of a difference in the strength of the primary selection force. It is obvious that there could be a need for a firmer connection between the upper jaw and the palate in some birds and consequently, these birds would have a more heavily fused palatine process. For example, the difference in the fusion of the palatine process in the several genera of woodhewers (Dendrocolaptidae) or between *Sapayoa* and the other genera of manakins (Pipridae) is probably the result of a difference in the strength of the primary selection force. However, this explanation accounts for only part of the variation. So long as the palatine process fulfills its primary function as an anchorage to which the palatine can fuse, then it does not matter what else happens to it. If the demands of the primary selection force are fulfilled and if there are no other selection forces acting on the palatine process (e.g., for a free process or for a lateral flange), then it would not seem to matter whether the process fuses completely to the prepalatine process, remains partly unfused or starts to degenerate into an isolated splint lying along the prepalatine process. Therefore, I will conclude that, except for the differences in the demands of the primary selection force, there seems to be no functional basis for the variation in the amount of fusion between the palatine process and the palatine, or in the development of the isolated splint. Since this variation in the degree of fusion lies within the limits of the primary selection force, the change from an unfused to a fused process does not appear to be an adaptive change. It would be, however, an evolutionary change, perhaps as pleitotropic expression of a complex gene system.

VARIATION OF THE PALATINE PROCESS OF THE PREMAXILLA

Having ascertained the embryological and the functional significance of the major variants of the palatine process of the premaxilla, it is now necessary to survey its occurrence and

variation throughout the Passeres. In this section, the structure of the palatine process will be recorded, genus by genus, for all but a few families of passerine birds. An attempt was made to separate the observed variation into its separate components — adult, individual, functional and so forth — but it is realized that the conclusions are provisional until good age series and samples of known adults are obtained. These components of variation are the most important part of this survey, and I will summarize them now instead of at the usual place at the end of the section.

The differences in the palatine process between families and occasionally between subfamilies and genera of passerine birds are chiefly functional ones of the type discussed in the preceding section. These variants with their functional interpretation follow.

a) The palatine process unfused to completely fused with the palatine. Slight variants of this series include (a) the anterior end of the process partly degenerate to degenerate, leaving the rest of the process isolated from the premaxilla, and (b) the posterior part of the palatine process fused to the dentary process of the premaxilla and/or to the maxilla. This series represents the stages associated with the varying strength of the primary function of the palatine process which is, of course, to provide a point of anchorage to which the palatine can fuse. When the palatine process fuses to the dentary process of the premaxilla, at least its anterior half fuses to the palatine. The exact reason for the fusion with the dentary process remains, however, unclear. The major problem of this variation in fusion is that it is identical to some aspects of age variation and to nonfunctional variation in the degree of fusion in the adult; these will be discussed below. No satisfactory means of separating these morphologically similar, but basically different, variants is available. Thus if a series of genera exhibit differences in the degree of fusion between the palatine process of the premaxilla and the prepalatine process, we cannot tell whether the variation is functional, or age variation. However, the differences in the degree of fusion between families, such as that between the heavy-billed icterids and the lighter-billed New World warblers, are frequently functional.

b) The distal end of the palatine process lying free of the prepalatine process and in the space between the palate and the jugal bar. The free process serves as the point of origin for part

of the M. pterygoideus which is apparently associated with rapid raising of the mandible.

c) A lateral flange developing at the site of fusion of the palatine process. The flange serves to distribute the shocks associated with cracking of seeds by the vise method employed by the cardueline and other groups of finches.

The variation of the palatine process within a family of passerine birds is commonly quite complex and must be carefully separated into its several components before offering any statements on the variation of the process within the family or the contained genera. Earlier authors (Lucas, 1894, p. 304; Amadon, 1950a, p. 214; and Tordoff, 1954a, p. 23) differ in their opinions on the amount of variation exhibited by the palatine process in a genus of passerine birds. However, their arguments are ambiguous for they did not separate the observed variation into its several components. The following types of variation can be expected when examining the palatine process within a family or genus of passerines.

a) All types of functional variation described above may occur between genera of a family, but they are infrequent. Examples may be: the differences in the fusion of the process in the several genera of woodhewers (Dendrocolaptidae) or between *Sapayoa* and the other genera of the manakins (Pipridae), or the free process in *Melopyrrha* and *Tiaris* and the lateral flange in *Oryzoborus* as compared to the normal palatine process seen in the other genera of emberizine finches. I do not know of any definite examples of functional differences between congeneric species.

b) Individual variation between adults of a species (or between adults of a genus as recorded in this study) is difficult to ascertain because of the variation in age. There are many examples in which there is no variation between the adults of a genus, usually when the process is completely fused in the adult. If the process is only partly fused in the adult, then it is impossible to determine the adult individual variation without a series of known adults. These were not available. Therefore, I will make the assumption for the purposes of the present study that there is no significant adult variation within genera of passerine birds. This assumption is obviously not correct, but it is very likely not far from the actual condition and it greatly simplifies the study of the minor variations in the degree of fusion between the palatine process and the surrounding bones.

c) The variation resulting from differences in the age of the specimens is of extreme importance because the final adult condition of the palatine process is not reached until the bird is between six months to a year old, because the expression of age variation is very similar to adult individual variation and to certain aspects of functional variation, and because many specimens in skeleton collections are birds less than a year old. Earlier workers have ignored age variation completely and as a consequence, have offered some erroneous conclusions on the amount of individual (adult) and even of functional variation. While examining the specimens used in the survey, I was able to separate some immature birds from adults on the basis of the ossification of the parietal windows and the general ossification of the skeleton, and to compare these groups for differences in the amount of fusion of the palatine process. In general, the palatine process becomes more fused with increasing age. The danger of age variation is that many genera are represented in collections by one or a few specimens so that there is no sure way of determining whether the structure has reached its final adult condition in the bird being examined and hence whether comparisons with other species are proper, i.e., adult with adult and not adult with immature. Realization of the dangers resulting from confusing age variation with adult individual or with functional variation has made me cautious in my discussions of the last two aspects of variation. Consequently, because much of the observed variation in the degree of fusion of the palatine process is the result of differences in the age of the specimens and because fewer erroneous conclusions can be based on age variation, I have assumed that all of the variation in fusion with the exception of obvious cases, such as between the genera of woodhewers, is the result of differences in the age of the specimens. Again, this assumption is possibly wrong, but it is the safest one to use until we have enough good series of specimens of known age.

Methods. The original survey and a major share of the study of the structure and variation of the palatine process of the premaxilla was carried out in the American Museum of Natural History — the entire passerine section of this skeleton collection was utilized. Subsequent study of material in the United States National Museum filled the gaps left after the original survey was completed. All in all, some 3300 specimens representing 500 genera of all but a few passerine families were examined. The missing families are all small groups which do not affect the

overall picture in the Passeres. I believe that an adequate sample of most families, certainly of all the important ones, was obtained. In addition to the Passeres, the Pici and the Coraciae were examined to acquire an idea of the structure of the palatine process in these groups that are believed to be the nearest relatives of the Passeres.

Only those skulls in which the rhamphotheca of the upper jaw and the membranes in the anterior half of the palate have been removed could be used in the survey. The faint suture separating the palatine process of the premaxilla and, in many cases, the palatine process itself is obscured if there is a thin layer of overlying tissue. A binocular microscope with a magnification of 10x to 15x was used in all examinations.

The structure and variation of the palatine process was determined in each genus available to me. Recording was done on the generic level because, with few exceptions, little or no variation was found between congeneric species; indeed, usually little variation was found between genera of the same family. Also in many cases, the specific identification was lacking or doubtful, and many old names were used so that the task of separating the species and determining the synonymies would have been far greater than justified by the returns. Particular attention was paid to age variation. I tried to assemble a large series of at least one genus in every family, from which the "typical" adult condition of the palatine process and the age variation was determined. The approximate age of the specimens was judged by the general degree of ossification of the skull and especially of the parietal windows (see Chapin, 1949, for a discussion of the parietal windows as a criterion of age in the passerines).

In the following synopsis, the structure of the palatine process is summarized for each family, and in a few cases for the subfamilies, of passerine birds. As mentioned above, the families will be listed according to the sequence to be used in "Peters' Check-list." Under each family (or subfamily) heading, a general description of the palatine process and of its major variation in that family is given. Usually one genus is chosen as the basis for description and comparison in the family. I have tried to choose for this purpose the genus having the most typical palatine process, but this genus is not to be regarded as the type of the family or even as completely typical for that family. If possible, the probable course of ontogenetic development is given. The genera examined are then listed. For each

genus, the number of specimens examined is given in parenthesis and a brief statement of the structure of the process is given. The genera within a family are listed alphabetically rather than according to supposed relationships. A far more complex problem is which generic names should be used. The labels on many specimens bore names no longer used; hence there was the huge task of synonymizing the discarded names with the currently accepted ones. The most convenient solution to this problem was to accept the most recent generic revision of each family. Peters (1951) was followed for the few groups of the suboscines treated in the last volume of his "Check-list." Hellmayr (1924-1938) was consulted for the remaining New World families, and various authors for the Old World groups. In some cases there has not been a recent revision of the family, and for these groups I have used the material in Mayr and Amadon (1951) or have followed the arrangement of genera used in the study collection in the American Museum of Natural History. In any event, the authority followed is cited for each group. I must emphasize that this system is used only because of convenience and not because I may advocate the generic limits set forth by these authors. Nor does it make much difference whether a broad or a narrow generic concept was employed in these revisions; the results of this paper would be the same with either concept.

The schematic drawings accompanying the descriptions (Figs. 23 to 28) show the left half of the upper jaw as seen from below. The arrow points to the palatine process of the premaxilla (labeled "P") or to the region of the fused palatine process. The figures are not drawn to scale.

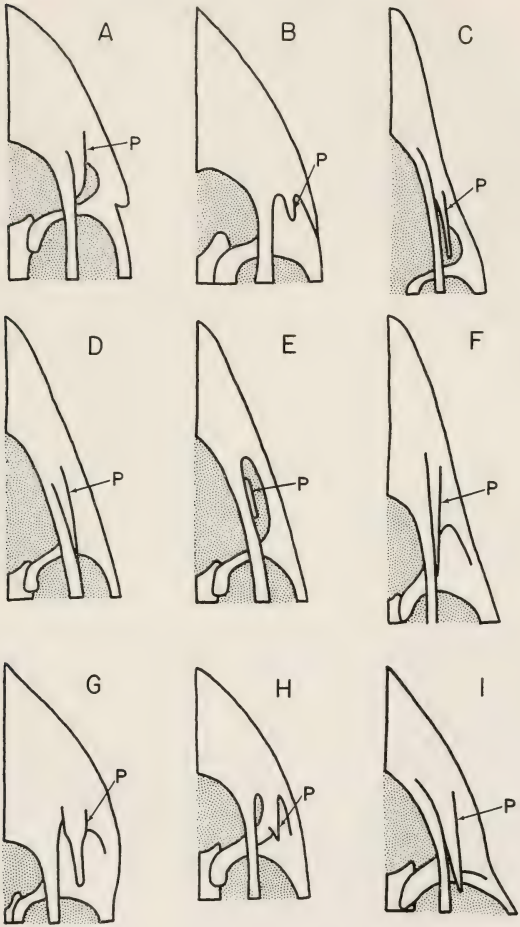

Figure 23. Palatine process of the premaxilla (P) of: (A) *Smithornis* (Eurylaimidae); (B) *Hypocnemis* (Formicariidae); (C) *Furnarius* (Furnariidae); (D) *Formicarius* (Formicariidae); (E) *Formicarius* (Formicariidae); (F) *Agriornis* (Tyrannidae); (G) *Tyrannus* (Tyrannidae); (H) *Cnipodectes* (Tyrannidae); and (I) *Euchlornis* (Cotingidae).

SYNOPSIS OF PASSERINE FAMILIES

Eurylaimidae

The process is present with a varying degree of fusion, from unfused up to the point of being completely lacking (= fused). "Lacking" is a neutral term and will be used when the process is not present as a visible structure, instead of the term "fused" which assumes that the process was present in the embryo and has become fused to the palate. In *Corydon*, the process is present and bears some resemblance to an ossified tendon (of the M. pterygoideus ?). All specimens of *Smithornis* (Fig. 23A) have the process, but the amount of fusion between it and the palate varies greatly. This may, in part, explain the absence of the process in *Calyptomena*, in which I have assumed that the palatine process is fused to the palatine. Lowe (1924) described and figured the palate of *Cymbirhynchus*, *Pseudocalyptomena* and *Smithornis*, but makes no mention of the process. Pycraft (1905a) did not mention the process in *Calyptura*, *Chasmorhynchus*, *Corydon*, and *Cymbirhynchus*, but did say that the anterior process of the palatine is broader where it joins the premaxilla which indicates that the process has fused to the palatines. Thus, it may be concluded that the typical adult condition of the palatine process in the broadbills is for the process to be fused to the palatines and that most, if not all, of the variation observed is because of differences in age and hence the degree of ossification.

Calyptomena (1), lacking; *Corydon* (2), present, somewhat resembles an ossified tendon; *Smithornis* (4), present, amount of fusion varies. Checked with Peters (1951).

Dendrocolaptidae

The process is present in all genera of woodhewers, but the amount of fusion between the process and the palatine varies greatly in the different genera. As a broad generalization, the process is only slightly fused in the long, curved-billed species and heavily fused in those species having a short, straighter and heavier bill. Some of the observed variation may be age, but some is almost certainly correlated with the strength of the bill.

Dendrocincla (2), heavily fused to palatine; *Dendrocolaptes* (1), slightly fused; *Drymornis* (1), slightly fused; *Glyphorynchus* (2), heavily fused; *Lepidocolaptes* (8), usually slightly fused, but some more fused; *Sittasomus* (2), slightly fused; *Xiphorhynchus* (22), usually slightly fused, but in the medium- to heavy-billed species, the process is as heavily fused as in *Dendrocincla*. Checked with Peters (1951).

Furnariidae

In most genera, the process is present, lying along the palatine and not fused with that bone. In *Furnarius* (Fig. 23C), the process lies free in the space between the palate and the dentary process of the premaxilla and in some ways resembles an ossified tendon. Rarely is the process fused

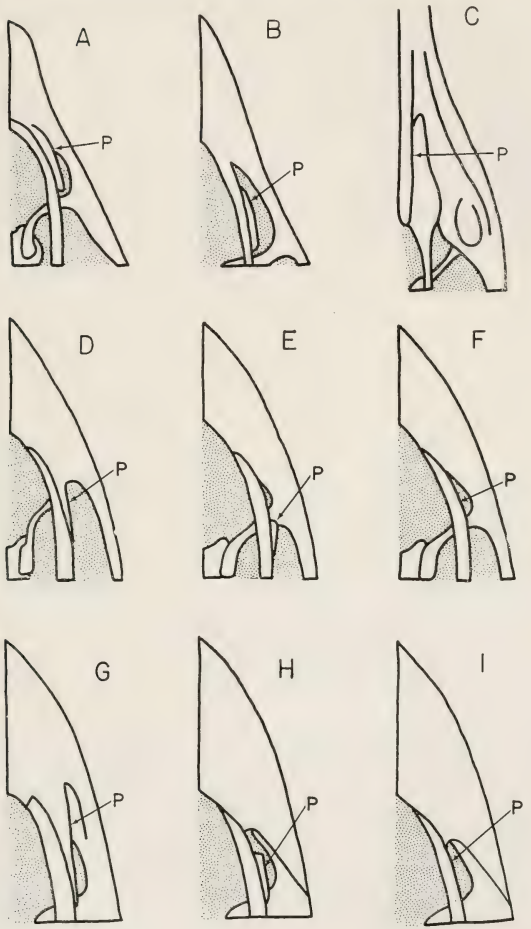

Figure 24. Palatine process of the premaxilla (P) of: (A) *Progne* (Hirundinidae); (B) *Anthus* (Motacillidae); (C) *Acanthorhynchus* (Meliphagidae, redrawn from Parker, 1877); (D) *Spizixos* (Pycnonotidae); (E) *Spizixos* (Pycnonotidae); (F) *Spizixos* (Pycnonotidae); (G) *Garrulax* (Timaliinae); (H) *Garrulax* (Timaliinae); and (I) *Garrulax* (Timaliinae).

or absent as in the case of *Leptasthenura* or *Synallaxis*. The length of the process varies somewhat between the genera.

Anabacerthia (2); *Anumbius* (1); *Aphrastura* (1), lacking ?; *Asthenes* (4); *Automolus* (5); *Chilia* (1), similar to *Furnarius*; *Cinclodes* (1); *Coryphistera* (1); *Cranioleuca* (4); *Furnarius* (22), present, usually lying in the space between the palate and the jugal bars, and reminiscent of an ossified tendon; *Geositta* (5); *Leptasthenura* (5), present, degree of fusion varies greatly; *Lochmias* (1), lacking ?; *Margarornis* (2); *Philydor* (1); *Phleocryptes* (3); *Premnoplex* (1); *Pseudocolaptes* (2); *Pseudoseisura* (2); *Sclerurus* (2); *Schoeniophylax* (1); *Synallaxis* (13), present, varies from unfused to fused; *Upucerthia* (4); *Xenops* (2). Process unfused unless otherwise noted. Checked with Peters (1951).

Formicariidae

The variation of the process in this family is almost as great as that seen in the entire order. In most genera, the process is present, lying along the palatine and scarcely fused to that bone, e.g., *Taraba*. In a few genera, such as *Hypocnemis* (Fig. 23B) and *Cercomacra*, the process lies in the space between the palate and the jugal bar, and seems to fuse, at least in part, with the overlying bone. A considerable amount of variation in the degree of fusion between the process and the palatine exists in some genera, such as *Thamnophilus*, *Phegopsis* and *Myrmorchilus*, in which the process varies from unfused to completely fused with the palatines. In *Formicarius* (Figs. 23D and 23E) the anterior end of the process degenerates until in some individuals only a small isolated splint of bone remains along the palatine. While much of the observed variation in the size and the degree of fusion is the result of age difference and hence of ossification, some of it probably represents true morphological difference between genera. However, no indication of relationships between the genera of the Formicariidae could be determined from the structure of the palatine process.

Cercomacra (5), present, unfused to fused to the palatine; *Chamaeza* (2); *Cymbilaimus* (2); *Dysithamnus* (2); *Formicarius* (5), present, unfused to degenerating at the anterior end to become an isolated splint lying along the palatine; *Formicivora* (7), lacking, no hint in any specimen; *Grallaria* (1); *Gymnopithys* (2); *Herpsilochmus* (1); *Hylophylax* (2); *Hypocnemis* (5) present, rather broad, unfused to fused, lying in the space between the palate and the jugal bar; *Microrhopias* (1) lacking ?; *Myrmeciza* (8), present, as in *Hypocnemis*, or lying next to the palatines; *Myrmorchilus* (2); *Myrmotherula* (6), present, unfused to fused, as in *Hypocnemis*; *Percnostola* (1); *Phaenostictus* (3), present, unfused to fused; *Phegopsis* (1), lacking ?; *Pyriglena* (2); *Sakesphorus* (3); *Taraba* (9); *Thamnophilus* (27), present, unfused to fused. Process unfused unless otherwise noted. Checked with Peters (1951).

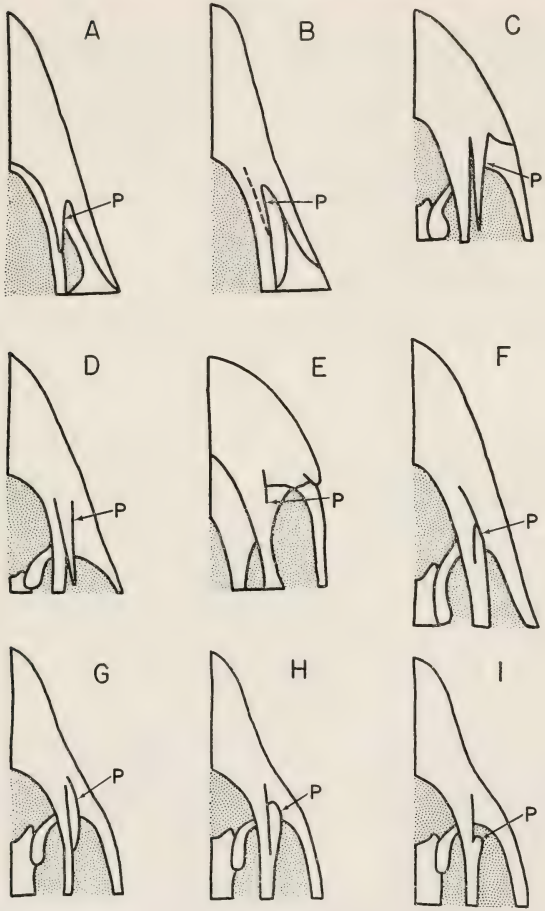

Figure 25. Palatine process of the premaxilla (P) of: (A) *Turdus* (Turdinae); (B) *Turdus* (Turdinae); (C) *Melopyrrha* (Emberizinae); (D) *Tiaris* (Emberizinae); (E) *Oryzoborus* (Emberizinae); (F) *Pipilo* (Emberizinae); (G) *Melospiza* (Emberizinae); (H) *Melospiza* (Emberizinae) and (I) *Melospiza* (Emberizinae).

Conopophagidae

Several specimens of this family were available for study, but unfortunately, the palates of all were damaged. In one skull, a very faint suture on the lateral side of the prepalatine process was seen — an indication that the process may be present, but partly fused with the palatine. Forbes (1881) figured the palate of *Conopophaga* in which the process was not shown. This, however, cannot be accepted as definite evidence that the process is lacking in this family because many authors were unaware of the existence of the process or otherwise failed to mention it.

Rhinocryptidae

The process is universally absent in all specimens examined in this family.

Pteroptochos (4); *Rhinocrypta* (1); *Scytalopus* (1). Process lacking. Checked with Peters (1951).

Cotingidae

The process is highly variable in this family; however, it must be remembered that the shape of the bill is also highly variable in the cotingas. The process may be present, but more commonly it is lacking (= fused to the palatine). When present, it usually lies next to the palatine, but in *Euchlornis* (Fig. 23I), it lies free in the space between the palate and the jugal bar. In *Cotinga*, the process may be partly fused to the dentary process of the premaxilla. How much of this variation in the fusion of the process to the surrounding bones is true difference between genera and how much is age variation cannot be determined, but certainly at least some is age. Thus, it is most likely that the adult condition of the palatine process for most genera of this family of broad-billed forms is a completely fused process and that those individuals having an unfused or a partly fused process are immature.

Ampelion (2); *Calyptura* (1); *Cephalopterus* (3); *Cotinga* (1); *Euchlornis* (4), present, long, lying free in the space between the palate and the jugal bar; *Gymnoderus* (1); *Lipaugus* (1); *Pachyramphus* (3), present, unfused in two specimens, fused in the other; *Procnias* (7); *Rupicola* (5); *Tityra* (3). Process lacking unless otherwise noted. Checked with Hellmayr (1929).

Pipridae

The process is present, short and unfused in all genera of this family, except for *Sapayoa* in which it is lacking (= fused). This genus is larger in size than the other manakins and has a broader bill which may account for its completely fused palatine process. This variation is in agreement with the generalization that the process is more fused in those forms with a heavier bill.

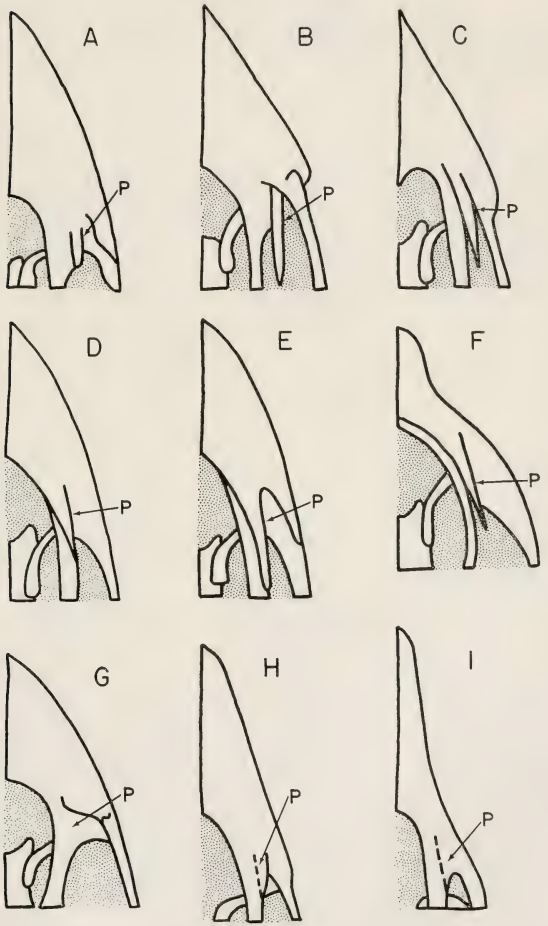

Figure 26. Palatine process of the premaxilla (P) of: (A) *Caryothraustes* (Cardinalinae); (B) *Spiza* (Cardinalinae); (C) *Piranga* (Tanagrinae); (D) *Thraupis* (Tanagrinae); (E) *Buthraupis* (Tanagrinae); (F) *Tersina* (Tersininae); (G) *Psittirostra* (Drepaniidae); (H) *Himatione* (Drepaniidae); and (I) *Vestiaria* (Drepaniidae).

Antilophia (1); *Chiroxiphia* (11); *Corapipo* (1); *Machaeropterus* (1); *Manacus* (4); *Pipra* (18); *Sapayoa* (2), lacking, no hint of the process; *Tyranneutes* (1). Process short and unfused unless otherwise noted. Checked with Hellmayr (1929).

Tyrannidae

The process varies greatly in this family of broad-billed birds. It may be present as a long process lying along the palatine (as in *Agriornis*, Fig. 23F) or as a short process at the base of the palatine (as in *Myiarchus*) or appear as an ossified tendon arising from the mass of bone at the junction between the palatine and the premaxilla or rarely from the maxillo-palatine (as in *Cnipodectes*, Fig. 23H) although it is not absolutely certain whether the short process on the maxillo-palatine is the palatine process), or may be completely absent (as in *Pitangus*). Even within a single genus, such as *Tyrannus*, the process may vary from being present to what appears as a tendinous process arising from the general mass of the premaxilla (Fig. 23G). The commonest condition is for the process to be lacking (= fused) or to vary in the degree of fusion with the palatine, but always with a tendency toward greater fusion. How much of the observed variation is age and how much is difference between genera is impossible to determine at this time. Certainly, at least some of the variation in fusion is age and some is functional.

Agriornis (6), unfused (long-billed form); *Arundinicola* (2); *Blacicus* (1); *Cnemotriccus* (7); *Cnipodectes* (1), present, attached to base of the maxillopalatine; *Colonia* (4); *Colopteryx* (4), varies as in *Tyrannus; Elaenia* (16), varies as in *Tyrannus; Empidonax* (30), usually lacking, but present in a few specimens; *Empidonomus* (3); *Entotriccus* (1); *Euscarthmornis* (1); *Fluvicola* (1); *Gubernetes* (1); *Knipolegus* (2); *Legatus* (1); *Lessonia* (4); *Lichenops* (2), lacking in one specimen, present in the other; *Lophotriccus* (1); *Mecocerculus* (2); *Megarynchus* (5), varies as in *Tyrannus; Muscisaxicola* (2); *Muscivora* (9), varies as in *Tyrannus; Myiarchus* (60), varies as in *Tyrannus; Myiobius* (1); *Myiochanes* (8), varies as in *Tyrannus; Myiophobus* (2); *Myiotheretes* (1), long as in *Agriornis, Myiozetetes* (24), varies as in *Tyrannus; Nuttallornis* (4); *Ochthoeca* (4); *Ochthornis* (1); *Oncostoma* (1); *Onychorhynchus* (2), varies as in *Tyrannus; Phaeomyias* (1); *Pipromorpha* (2) varies as in *Tyrannus; Pitangus* (20), varies as in *Tyrannus*, but most have a free process; *Pseudocolopteryx* (1); *Pyrocephalus* (23); *Pyrrhomyias* (2); *Rhynchocyclus* (1); *Sayornis* (11); *Serpophaga* (3); *Sirystes* (2), varies as in *Tryannus; Snethlagea* (1); *Spizitornis* (3); *Sublegatus* (2); *Suiriri* (1); *Todirostrum* (3); *Tolmarchus* (13), varies as in *Tyrannus; Tolmomyias* (4); *Tyranniscus* (5), varies as in *Tyrannus; Tyrannulus* (1); *Tryannus* (52), present, to degenerating to what appears as a tendinous process arising from the general mass of bone of the premaxilla (this can be easily broken and is lost in many specimens); *Xolmis* (5), unfused and long in one specimen, lacking in the others. Process lacking unless otherwise noted. Checked with Hellmayr (1927).

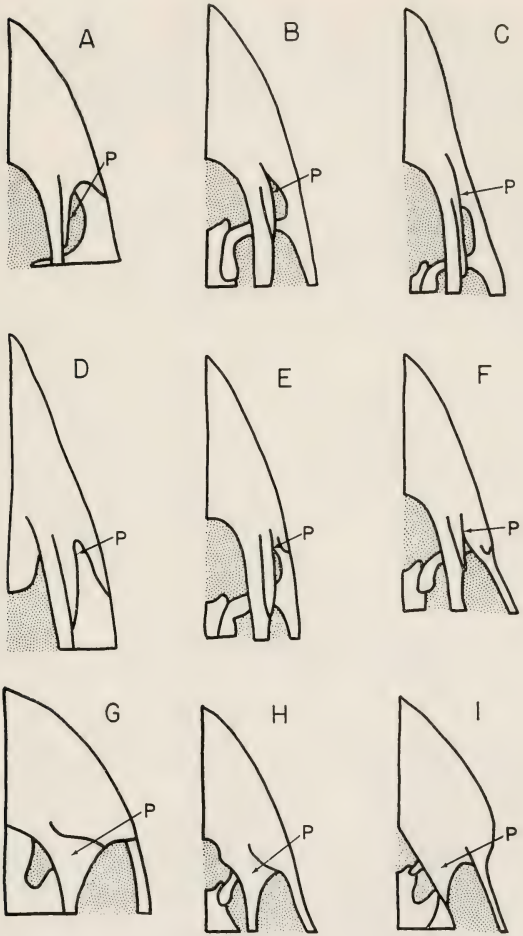

Figure 27. Palatine process of the premaxilla (P) of: (A) *Vireo* (Vireonidae); (B) *Icteria* (Parulidae); (C) *Euphagus* (Icteridae); (D) *Gymnostinops* (Icteridae); (E) *Quiscalus* (Icteridae); (F) *Fringilla* (Fringillinae); (G) *Coccothraustes* (Carduelinae); (H) *Carduelis* (Carduelinae); and (I) *Lonchura* (Estrildidae).

Oxyruncidae

One badly preserved specimen was available for study. The process is apparently lacking, but because of the condition of the specimen, there is still some question as to the true condition of the process.

Oxyruncus (1), lacking ?. Checked with Hellmayr (1929).

Phytotomidae

The process is absent in all specimens of this monotypic family and may be fused, at least in part, with the dentary process of the premaxilla instead of with the palatine. *Phytotoma* is a heavy-billed bird so that its fused process provides additional evidence for the generalization that the process fuses completely with the surrounding bones in heavy-billed birds.

Phytotoma (9), lacking (fused with the dentary process of the premaxilla ?). Checked with Hellmayr (1929).

Pittidae

The process is present, but varies from being partly fused to completely fused with the palatine. The bill is approximately the same shape and size in all specimens, therefore this variation is most likely age and not the result of functional differences. Consequently, the typical adult condition is assumed to be a completely fused process and those specimens with a partly fused process are probably immature birds.

Pitta (18), unfused in 11 specimens, lacking in the other 7. Checked with Peters (1951).

Xenicidae

No specimens of this rare family were available for study. Forbes (1882) did not mention this process in his paper on the anatomy of *Xenicus* and *Acanthisitta*. Pycraft (1905b) described and figured the palate of *Acanthisitta*, but also did not mention the process.

Philepittidae

No specimens of this family were available for study. Forbes (1880) reported on the anatomy of *Philepitta* and figured the palate in which the process was not shown.

Menuridae

The process is lacking in this group of large birds with relatively heavy bills.

Menura (2), lacking. Checked with Mayr and Amadon (1951).

Atrichornithidae

No specimens of this rare family were available for study. The only anatomical study of *Atrichornis* that I know of is by Garrod (1877), but unfortunately he does not describe the palate.

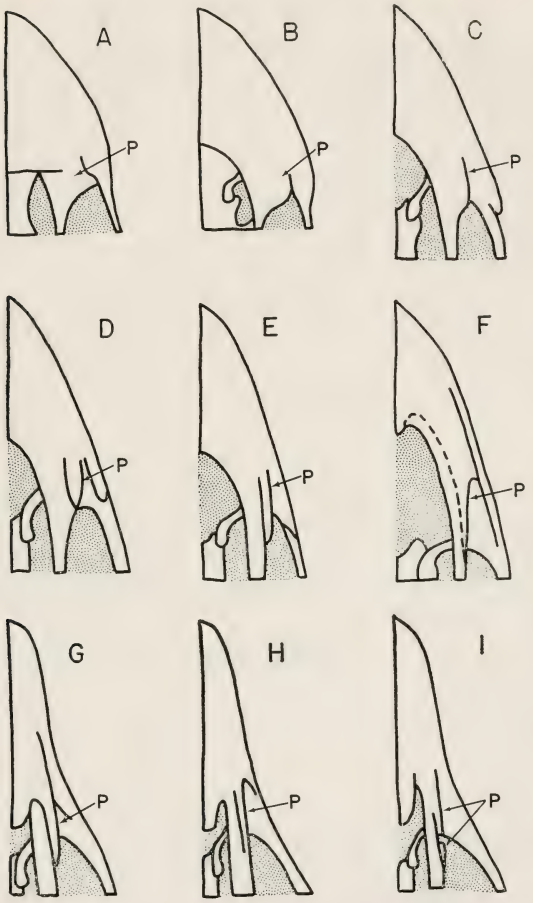

Figure 28. Palatine process of the premaxilla (P) of: (A) *Spermospiza* (Estrildidae); (B) *Ploceus* (Ploceidae); (C) *Passer* (Ploceidae); (D) *Dinemellia* (Ploceidae); (E) *Bubalornis* (Ploceidae); (F) *Cyanocitta* (Corvidae); (G) *Paradisaea* (Paradisaeidae); (H) *Paradisaea* (Paradisaeidae); and (I) *Paradisaea* (Paradisaeidae).

Alaudidae

The process is present in most genera of larks, but there is much variation in the degree of fusion between it and the palatine. In some genera, such as *Eremophila*, the process is completely lacking (= fused). When present, the process usually lies along the palatine, but in *Melanocorypha*, it lies free in the space between the palate and the jugal bar. *Certhilauda* has a long, decurved bill and lacks the process. This is the opposite of the condition found in many groups in which the heavy-billed forms lack the process and the species with long, thin or decurved bills have a well-developed process. However, *Certhilauda* uses its bill to dig in the ground (Meinertzhagen, 1951, p. 101) and the fused process probably gives the bill greater strength as in the thrashers (*Toxostoma*).

Alauda (8), degree of fusion varies; *Calandrella* (1), process almost completely fused with the palatine and the jugal bar; *Certhilauda* (1), lacking; *Eremophila* (17), lacking; *Eremopterix* (3), unfused; *Lullula* (1), lacking; *Melanocorypha* (1), process lying free in space between the palate and the jugal bar; *Mirafra* (5), partly fused to the palatine. Checked with Vaurie (1951) and Meinertzhagen (1951).

Hirundinidae

Most genera of swallows have a well-developed process which lies next to the palatine and is not fused at all with that bone (Fig. 24A). In *Iridoprocne*, the degree of fusion varies from unfused to completely fused with the palatine. All specimens of *Hirundo* lacked the process. The bill of all genera of swallows is equally broad and apparently similar in function so that the significance of the variation in *Iridoprocne* and *Hirundo* remains a mystery.

Atticora (2); *Delichon* (4); *Hirundo* (22), lacking; *Iridoprocne* (20), present, but varies from unfused to completely fused; *Lamprochelidon* (1); *Orochelidon* (1); *Petrochelidon* (6); *Phaeoprogne* (2); *Progne* (14); *Riparia* (5); *Stelgidopteryx* (10); *Tachycineta* (2). Process present and unfused unless otherwise noted. Checked with Hellmayr (1935) and with Mayr and Bond (1943).

Motacillidae

In this family of thin-billed species, the process is lost except for a thin isolated splint of bone lying along the palatines in some specimens (Fig. 24B). This splint can be easily broken off, so that it is not known how much of the observed variation is natural and how much is artificial.

Anthus (36), usually lacking, but in a few specimens there is an indication of an isolated splint lying along the palatine; *Macronyx* (3), isolated splint in one specimen, lacking in the others; *Motacilla* (33), lacking or present as a splint lying along the palatine. Checked against the A.M.N.H. collection.

Campephagidae

In a few genera of the cuckoo-shrikes, such as *Campephaga*, there is a short process at the anterior end of the palatines. In most genera, however, the process fuses to the palatines. This seems to be the typical adult condition in this family and the observed variation in fusion appears to be age variation.

Campephaga (4), short, unfused; *Coracina* (8), lacking; *Edolisoma* (2), lacking; *Hemipus* (2), lacking; *Lalaga* (1), present (?), short; *Pericrocotus* (43), lacking, but in a few specimens there is a hint of a process; *Volvocivora* (1), short, partly fused. Checked against the A.M.N.H. collection.

Pycnonotidae

The process varies from being present and unfused to completely fused in the bulbuls. In general, it fuses partly to the prepalatine process to form a large part of that bone and partly to the dentary process of the premaxilla. In a few genera, such as *Spizixos* (Figs. 24D, 24E, and 24F), the process degenerates at its anterior end to become a thin, isolated splint of bone lying along the palatine, such as in *Paradisaea* or in *Motacilla*. Except for the difference between the *Microscelis*-type and the *Spizixos*-type, the variation in the degree of fusion between the process and the palatine is probably age variation; the difference between *Spizixos* and *Microscelis* is probably functional, but more than that I cannot say.

Baeopogon (4); *Bleda* (5); *Calyptocichla* (2); *Criniger* (6); *Ixonotus* (1), lacking ?; *Microscelis* (33); *Phyllastrephus* (4); *Pycnonotus* (93); *Spizixos* (26), present, the anterior end generally degenerating to an isolated splint lying along the palatine; *Thescelocichla* (2); *Trachycomus* (5). Unless otherwise stated, the process varies from unfused to fused with the prepalatine process and, in part, to the dentary process of the premaxilla. Checked with Delacour (1943a).

Irenidae

The nature and variation of the process in this family is identical to that in the closely related Pycnonotidae.

Aegithina (8), partly fused to completely fused with the palatine; *Chloropsis* (8), lacking; *Irena* (8), partly fused to completely fused with the palatine. Checked with Mayr and Amadon (1951).

Laniidae

The process is lacking (= fused) in most members of this heavy-billed family. A few specimens, however, have a small, partly fused process at the anterior end of the palatine, which indicates that the process fuses with the palatine and that any variation is probably due to age.

Dryoscopus (6), lacking; *Laniarius* (13), lacking, one specimen had a faint suture showing that the process had fused to the palatine; *Lanius*

(13), partly fused to completely fused; *Malaconotus* (3) lacking; *Pelicinius* (1), long, partly fused to the palatine; *Rhodophoneus* (1), lacking; *Tchagra* (3), one specimen had a long, partly fused process, the other lacked the process; *Urolestes* (2), lacking. Checked against the A.M.N.H. collection.

Prionopidae

No specimens of this family were available for study, nor could I find a description of the palate in the literature. It is most likely that they agree with the Laniidae in the structure of the process. Genera checked with Mayr (1943).

Vangidae

No specimens of the vanga shrikes were available for study, nor could I find a description of their palate in the literature. It is most probable that the structure of the process in the vangids is the same as in the true shrikes.

Bombycillidae

The process is lacking in all but a few specimens of this family. These latter specimens, especially the two individuals of *Dulus*, are probably immature birds in which the process is less fused to the palatine. As in the preceding families, the observed variation is the result of a difference in age and hence in ossification.

Bombycilla (33), lacking or a faint indication in a few specimens; *Dulus* (10), usually lacking, but two specimens had a well-developed process; *Phainopepla* (9), lacking; *Ptilogonys* (5), lacking. Checked with Mayr and Amadon (1951) and with Delacour and Amadon (1949).

Cinclidae

As in the closely related thrushes, the process in the dipper is lacking as a distinct structure in the adult and is assumed to be fused with the palatine.

Cinclus (7), lacking. Checked with Mayr and Amadon (1951).

Troglodytidae

Most specimens examined lacked a process; however, in a few genera, such as *Heleodytes*, *Cinnycerthia* and *Thryothorus*, the process varies from being present, but partly fused, to completely fused with the palatine. It appears that the adult conditon is complete fusion and that the observed variation is due to age.

Catherpes (2); *Cinnycerthia* (8), varies as in *Heleodytes; Cistothorus* (4); *Heleodytes* (15), partly fused to completely fused with the palatine; *Henicorhina* (1); *Leucolepis* (1); *Salpinctes* (6); *Thryomanes* (1); *Thryothorus* (55), varies as in *Heleodytes; Troglodytes* (31). Process lacking unless otherwise noted. Checked with Hellmayr (1934).

Mimidae

Except for *Margarops,* the process is lacking (= fused) or heavily fused with the palatine in all genera of the mimids. Individuals having a partly fused process are, with little doubt, immature birds and the variation in the degree of fusion is thus due to age. In the case of *Margarops,* however, it seems likely that the process is present and not fused to the palatine in the adult bird (that is, the four birds examined are not immature), but the significance of this difference between *Margarops* and the rest of the mimids is not known.

Allenia (2); *Cinclocerthia* (1); *Donacobius* (1); *Dumetella* (13), a hint of the process in a few specimens, and in one specimen the process was only slightly fused; *Margarops* (4), unfused, lying next to the palatine, *Melanoptila* (1); *Melanotis* (3); *Mimodes* (1); *Mimus* (7); *Nesomimus* (3); *Oreoscoptes* (2); *Toxostoma* (8). Process lacking unless otherwise noted. Checked with Hellmayr (1934).

Prunellidae

The process is lacking in *Prunella* as in the closely related Turdinae.

Prunella (5), lacking. Checked with Marien (1951).

Turdinae

The process is usually fused to one or more of the surrounding bones (the palatine or the dentary process of the premaxilla). In a few genera, such as *Hylocichla* or *Turdus,* a partly fused process is present in some specimens which are assumed to be young birds (Fig. 25A and 25B). Hence, the fused process is the adult condition and any variation in the degree of fusion is mostly likely due to differences in age.

Alethe (4); *Callene* (2); *Cichladusa* (18); *Copsychus* (18); *Cossypha* (5); *Enicurus* (12); *Erithacus* (31); *Erythropygia* (1); *Hylocichla* (18), a faint indication of the process in a few specimens; *Monticola* (1); *Myadestes* (3); *Neocossyphus* (2); *Oenanthe* (4); *Phaeornis* (1); *Phoenicurus* (16); *Saxicola* (25); *Sialia* (15); *Thamnolaea* (2); *Turdus* (19), a faint indication of the process in a few specimens and a partly fused process in two others; *Zoothera* (2). Process lacking unless otherwise noted. Checked with Ripley (1952).

Timaliinae

The variation of the process in either *Garrulax* (Figs. 24G, 24H, 24I) or *Liothrix* is typical for this subfamily. In these genera, the process varies from being present and unfused to fused with any of the surrounding bones (palatine, or the dentary process of the premaxilla). The adult condition is thus assumed to be a completely or an almost completely fused process and the observed variation in the degree of fusion to be due to age.

Alcippe (19), varies as in *Liothrix; Babax* (4), varies as in *Garrulax; Chamaea* (5), lacking; *Chrysomma* (1), unfused, lying along the palatine; *Dumetia* (1), fused to dentary process of the premaxilla; *Gampsorhynchus* (1), fused to dentary process of the premaxilla; *Garrulax* (55), unfused to fused with the dentary process of the premaxilla, process also partly overlies the palatine; *Heterophasia* (3), fused to the dentary process; *Lioptila* (4), varies as in *Liothrix; Liothrix* (38), long and unfused, with the anterior end fusing to the dentary process, and thus leaving an isolated splint of bone (the posterior end of the process) lying along the palatine; *Macronus* (4), fused to the dentary process; *Malacocincla* (5), varies as in *Garrulax; Malia* (1), varies as in *Garrulax; Pellorneum* (1), fused to the dentary process; *Pomatorhinus* (7), varies as in *Liothrix; Psophodes* (2), varies as in *Garrulax; Pteruthius* (5), varies as in *Garrulax; Rhinocichla* (1), heavily fused to the palatine; *Siva* (10), varies as in *Liothrix; Stachyris* (6), varies as in *Liothrix; Trochalopteron* (25), varies as in *Garrulax; Turdoides* (2), varies as in *Garrulax; Yuhina* (26), varies as in *Liothrix*. Checked with Delacour (1946).

Paradoxornithinae

The process is lacking in the one genus examined in this subfamily and it is assumed to be fused as in the closely related Timaliinae.

Suthora (5), lacking. Checked with Delacour (1946).

Polioptilinae

The process is lacking (= fused) in this group of thin-billed birds and is similar to that seen in the closely related Sylviinae.

Microbates (4), lacking, but with a hint of a fused process; *Polioptila* (10), lacking; *Ramphocaenus* (1), lacking. Checked with Rand and Traylor (1953).

Sylviinae

The process is lacking (= fused) in almost all genera of this subfamily. In a few genera, such as *Cisticola* and *Prinia*, an unfused process is present in some specimens. This indicates that the typical adult condition is for the process to be fused with the palatine and that the observed variation in the degree of fusion is age variation.

Abroscopus (3); *Acrocephalus* (9); *Apalis* (2); *Bradornis* (5), (may be a muscicapiine?); *Camaroptera* (2); *Cisticola* (9), present as a long thin process that is partly or completely fused to the palatine; *Eremomela* (2), present in one specimen, lacking in the other; *Franklinia* (3); *Hylia* (1); *Hypergerus* (2); *Oreopneuste* (1); *Phragamaticola* (1); *Phylloscopus* (23), a small splint of bone lying along the palatine in one specimen, signs of a fused process in a few other specimens; *Prinia* (10), present, small, at the very anterior end of the palatine, partly fused in two specimens; *Regulus* (27); *Seicercus* (1); *Sylvia* (6); *Sylvietta* (2); *Tribura* (8); *Urosphena* (1). Process lacking unless otherwise noted. Checked against the A.M.N.H. collection.

Malurinae

The process is lacking in the Malurinae.

Malurus (1), lacking. Checked with Mayr and Amadon (1951).

Muscicapinae

The process is almost universally lacking in the Old World flycatchers, but there is a hint of a process in a few specimens, e.g., *Culicicapa,* which indicates that the broad anterior end of the palatine process is composed in part of the fused process. Thus the adult condition is for the process to be fused and any variation in fusion is most likely age variation.

Batis (2); *Bias* (2); *Culicicapa* (5), hint of a fused process in one specimen; *Erranornis* (2); *Erythocercus* (1); *Ficedula* (11); *Fraseria* (2); *Hyliota* (1); *Muscicapa* (10); *Niltava* (4); *Platysteira* (1). Process lacking. Checked with Vaurie (1953) and against the A.M.N.H. collection.

Monarchinae

The process is lacking as in the closely related Muscicapinae.

Chasiempis (1); *Hypothymis* (7); *Terpsiphone* (11); *Trochocercus* (2). Process lacking. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Pachycephalinae

The process is lacking in this group of heavy-billed flycatchers.

Colluricincla (2); *Eopsaltria* (1); *Falcunculus* (1); *Pachycephala* (4). Process lacking. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Paridae

A short process is present in some individuals which becomes fused, in part with the dentary process of the premaxilla, but mainly with the palatine in the adult. The variation in the degree of fusion is assumed to be age and hence ossification.

Aegithaliscus (3); *Aegithalos* (2); *Parus,* a partly fused process is present in a few specimens; *Psaltriparus* (6). Process lacking. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Sittidae

The process is lacking in all specimens of this heavy-billed family. However, in one specimen of *Sitta,* there is a suggestion of a suture on the prepalatine process indicating that the process has fused with the palatine.

Rhabdornis (1); *Sitta* (49); *Tichodroma* (1). Process lacking. Checked with Mayr and Amadon (1951).

Certhiidae

The process is lacking (= fused) in most specimens of this thin-billed genus, this being the typical adult condition. In one specimen, however, the process is only partly fused to the palatine which indicates that the process is present and unfused in the immature and becomes increasingly fused with age.

Certhia (17), lacking, but a slight indication of the process in one specimen. Checked with Mayr and Amadon (1951).

Dicaeidae

The typical condition of the process in this thin-billed family is a thin isolated splint lying along the palatine. In some specimens, presumably immatures, the process is still attached to the premaxilla. In others, the anterior connection to the premaxilla has degenerated toward the typical adult condition. If the process is lacking, it is most likely the result of loss during preparation, although the process could degenerate completely in some specimens.

Dicaeum (7), lacking or as a splint lying along the palatine. Checked with Mayr and Amadon (1947).

Nectariniidae

The process is usually lacking in this family of long, thin-billed birds. In a few specimens, there is a slight suggestion that the process has become fused to the palatine during development.

Aethopyga (3); *Anthreptes* (2); *Arachnothera* (2); *Nectarinia* (23), a slight indication of the process in a few specimens. Process lacking. Checked with Delacour (1944).

Zosteropidae

The process is usually lacking in this family of short thin-billed species with the usual indication of a semifused process in a few specimens.

Zosterops (15), usually lacking. Checked with Mayr and Amadon (1951).

Meliphagidae

The process is lacking (= fused) in most specimens of this family. In *Philemon,* however, the process is present, but at least partly fused to the palatine. Thus it is evident that in the adult of this family, the process fuses to the prepalatine process and that any variation in fusion is probably due to age.

Parker (1877) reported that the palatine process in *Acanthorhynchus* (Fig. 24C) lies along the medial side of the palatine. This is possible, although the specimen of the genus that I examined did not show this

condition. I was careful to check specimens of the entire order for additional examples in which the palatine process lay on the inside rather than on the outside of the palatine, but could not find any such specimens. Thus, I would suggest that the palatine process in *Acanthorhynchus* is normal and lies on the lateral side of the palatine.

Acanthorhynchus (1); *Conopophila* (1); *Melilestes* (1); *Meliornis* (2); *Meliphaga* (2); *Melithreptus* (2); *Myzantha* (1); *Myzomela* (3); *Philemon* (6), present, but partly fused to the palatine. Process lacking unless otherwise noted. Checked against the A.M.N.H. collection.

Emberizinae

The process varies greatly in this group of finches. Typically, it lies next to the palatines and is more or less fused to that bone, but in a number of specimens, it is completely fused (Fig. 25F). The figures of *Melospiza melodia* (Figs. 25G, 25H, and 25I) illustrate what seems to be the typical course of reduction and fusion of the process with increase in age; however, the process can also fuse to the palatine without any reduction in size. In *Melopyrrha* (Fig. 25C) and *Tiaris* (Fig. 25D), the process lies free in the space between the palate and the jugal bar and appears similar to that seen in the cardinals. In *Oryzoborus* (Fig. 25E), a very heavy-billed species, the process is completely fused to the palatine and in its place is a lateral flange similar to that seen in the Carduelinae. Much of the observed variation in this family is no doubt age variation, but aside from *Melopyrrha*, *Tiaris*, and *Oryzoborus* which are special problems, it is difficult to determine the fully adult condition in the different genera. Hence the significance, both taxonomically and functionally, of the variation in fusion cannot be evaluated at this time.

Ammospiza (7), unfused to almost completely fused; *Arremonops* (1), lacking; *Calcarius* (1), lacking ?; *Emberiza* (6), slightly fused; *Guiraca* (4), slightly fused; *Junco* (8), slightly fused; *Melopyrrha* (2), lying free in the space between the palate and the jugal bar; *Melospiza* (16), slightly fused to completely fused, specimens show reduction of the anterior end of the process; *Oryzoborus* (3), lacking, anterior end of palatine has a lateral flange; *Paroaria* (10) slightly fused to almost completely fused; *Passerculus* (9), partly fused to completely fused; *Passerella* (7), lacking, some specimens with a faint suture; *Phrygilus* (1), slightly fused *Pipilo* (9), partly fused to completely fused; *Plectrophenax* (7), slightly fused; *Pooecetes* (1), lacking; *Sicalis* (1), lacking; *Spizella* (7), slightly to partly fused; *Sporophila* (7), lacking, one specimen showed a hint of the process; *Tiaris* (1), free as in *Melopyrrha*; *Zonotrichia* (15), slightly fused. Checked with Tordoff (1954a).

Cardinalinae

The process is present in all genera of this heavy-billed group of finches. Usually it lies free in the space between the palate and the jugal bar (Figs. 3 and 26B), but in some genera, such as *Caryothraustes*

(Fig. 26A) and *Saltator*, the process lies along the palatines. There may or may not be a suture between the free process and the rest of the premaxilla, but the process never fuses to the palatine. At the present time, none of the observed variation can be correlated with any functional or taxonomic significance.

Cardinalis (14), free; *Caryothraustes* (1), lying along the palatine; *Guiraca* (3), free; *Passerina* (7), free; *Pheucticus* (9), free; *Saltator* (8), in some specimens it lies free, in others it lies along the palatine; *Spiza* (1), free (may be icterid). Checked with Tordoff (1954a).

Tanagrinae

The process is present in all specimens of tanagers that were examined. It may lie in the space between the palate and the jugal bar, but usually it lies along the palatine although the two bones apparently do not fuse (Figs. 26C, 26D, and 26E). A suture separating the process from the rest of the premaxilla may or may not be present. Tordoff reports the process as being partly fused to the palatine with a suture present; this does not agree with my findings that the process does not fuse at all with the palatine. However, because of the difficulty of determining the degree of fusion between the process and the palatine by examination of the ventral aspect of the palate, this difference of interpretation is of no importance.

Buthraupis (1); *Calospiza* (9); *Chlorophonia* (1); *Chlorospingus* (1), lying free; *Compsocoma* (1); *Habia* (1); *Hemithraupis* (1); *Orthogonys* (1); *Poecilothraupis* (2); *Pipraeidea* (2); *Piranga* (9), lying free; *Ramphocelus* (2); *Schistochlamys* (3); *Spindalis* (2); *Tachyphonus* (3); *Tangara* (21); *Tanagra* (8). Process present, unfused or free. Checked with Hellmayr (1936).

Tersininae

The process is present in this swallow-billed species. It lies somewhat free in the space between the palate and the jugal bar, but still closely attached to the palatine (Fig. 26F). In general, the process resembles that seen in the true swallows.

Tersina (3), unfused, lying somewhat free. Checked with Hellmayr (1936).

Coerebinae

The process is present in this group of thin-billed birds. It always lies against the palatine, but its length varies as does the degree of fusion with the palatine, which varies from slightly fused to completely fused. How much of the variation in the degree of fusion is age variation and how much represents a true difference between genera is unknown.

Ateleodacnis (4), heavily to completely fused; *Chlorophanes* (3), long, slightly to completely fused; *Coereba* (12), short, partly to completely fused; *Conirostrum* (2), long, slightly fused; *Cyanerpes* (24), long, slightly

(usually) to heavily fused; *Dacnis* (4), slightly to strongly fused; *Diglossa* (3), long, partly fused; *Eumcornis* (2), short, not fused. Checked with Hellmayr (1935).

Catamblyrhynchinae

The process is lacking (= fused) in this heavy finch-billed genus. *Catamblyrhynchus* (2), lacking. Checked with Hellmayr (1938).

Parulidae

In this family of thin-billed birds, the process is present as a thin splint lying along the palatine (Fig. 27B). It degenerates at its anterior end and becomes fused to the palatine with increasing age. The fully adult condition is apparently for the process to be heavily fused with the palatine; hence the observed variation in fusion is most probably age variation.

Dendroica (79); *Geothlypis* (8); *Helmitheros* (3); *Icteria* (4); *Mniotilta* (12); *Parula* (2); *Protonotaria* (2); *Oporornis* (10); *Seiurus* (34); *Setophaga* (10); *Vermivora* (13); *Wilsonia* (10). Process present, lying along the palatine with the anterior end degenerating to leave a thin splint which finally fuses with the palatine. Checked with Hellmayr (1935).

Drepaniidae

In the heavy, finch-billed genus, *Psittirostra* (Fig. 26G), the process and the anterior half of the palate is exactly like that in the cardueline finches. In the other genera, the process is lacking (= fused), but the anterior end of the palatine does not flare out to the side as strongly as in *Psittirostra*, and in some there is no flaring of the palatine (Figs. 26H, and 26I). In at least one specimen, that of *Hemignathus*, a faint suture is present on the lateral half of the prepalatine process, which indicates that the process is present, but has fused completely to the palatine.

Hemignathus (1), long, curved-bill; *Himatione* (3), short, medium-bill; *Loxops* (1), short, thin-bill; *Psittirostra* (9), lateral flange present, bill similar to cardueline bill; *Vestiaria* (1), medium, curved-bill. Process lacking. Checked with Amadon (1950a).

Vireonidae

The process is lacking (= fused) in all specimens of vireos (Fig. 27A), except for one in which the process is visible but heavily fused to the palatine. This indicates that the process is present in the immature and becomes fused with the palatine with increasing age. The process is lacking in *Cyclarhis*, a heavy-billed species. I was unable to examine any specimen of *Vireolanius*, another heavy-billed species, but presumably the process of this genus would be similar to that seen in *Vireo* and *Cyclarhis*.

Cyclarhis (7), lacking; *Vireo* (16), lacking in all but one specimen which showed a faint suture. Checked with Hellmayr (1935).

Icteridae

The process is lacking (= fused) in most specimens examined in this family. In some specimens, however, e.g., *Euphagus, Gymnomystax, Icterus, Xanthornus* and *Quiscalus,* the process is absent, but usually heavily fused with the palatine (Figs. 27C, 27D, and 27E). This variation is, no doubt, mainly due to differences in age; the adult condition is presumed to be complete fusion between the process and the palatine.

Agelaius (6), suture sometimes weakly present; *Amblycercus* (2); *Cacicus* (3); *Dolichonyx* (4); *Euphagus* (3), present, slightly fused to almost completely fused; *Gnorimopsar* (1); *Gymnomystax* (2), suture very faint; *Gymnostinops* (2); *Holoquiscalus* (1), with a faint suture; *Hypopyrrhus* (1), present, but heavily fused; *Icterus* (22); heavily fused in some specimens; *Molothrus* (7); *Notiopsar* (2); *Pezites* (3); *Psomocolax* (1); *Quiscalus* (15), heavily fused in some specimens; *Sturnella* (6), suture sometimes weakly present; *Tangavius* (1); *Xanthocephalus* (1); *Xanthornus* (1), faint suture; *Zarhynchus* (1). Process lacking unless otherwise noted. Checked with Hellmayr (1937).

Fringillinae

In *Fringilla,* the process is present and lies along the palatine, much the same as that seen in many genera of the Emberizinae. However, it may be even less fused with the palatine than in that group (Fig. 27F).

Fringilla (3), present, slightly fused, lying along the palatine. Checked with Mayr *et al.* (1956).

Carduelinae

The process is lacking (= fused) in all specimens of this group of heavy-billed finches. In addition, the anterior end of the prepalatine process bears a lateral flange (Figs. 4, 27G, and 27H).

Carduelis (including *Acanthis* and *Spinus* specimens) (18); *Carpodacus* (14); *Chloris* (3); *Coccothraustes* (3); *Eophona* (2); *Hesperiphona* (19); *Leucosticte* (6); *Loxia* (6); *Pinicola* (3); *Poliospiza* (2); *Pyrrhula* (1); *Serinus* (12). Process lacking, but lateral flange present. Checked with Mayr and Amadon (1951) and against the A.M.N.H. collection.

Estrildidae

All specimens examined had a lateral flange similar to that in the Carduelinae (Figs. 27I, and 28A). As in that group, it is assumed that the process has fused with the palatine to form part of the lateral flange.

Amadina (4); *Clytopiza* (1); *Erythrura* (2); *Estrilda* (14); *Lonchura* (16); *Poephila* (11); *Pytilia* (3); *Pyrenestes* (1); *Spermophaga* (1); *Steganopleura* (4). Process lacking, but lateral flange present. Checked with Delacour (1943b).

Bubalornithinae

The process is present in *Bubalornis* and *Dinemellia* (Figs. 28D, and 28E) as reported earlier by Sushkin (1927). In these genera, the process lies next to the palatine and is partly fused with that bone.

Bubalornis (1), present, but heavily fused; *Dinemellia* (3), present, lying next to the palatine, slightly to partly fused.

Passerinae

The process is usually lacking (= fused) in this subfamily (Fig. 28C). It may be present in some specimens as a heavily fused process, but the sutures are so faint that it is difficult to determine their true nature.

Passer (15), lacking.

Ploceinae

The process is lacking in this subfamily of weaver finches. The anterior part of the prepalatine process flares out to the side as in the carduelines.

Anaplectes (1); *Coliuspasser* (3); *Diatropura* (2); *Euplectes* (9); *Malimbus* (1); *Plocepasser* (2); *Ploceus* (7); *Pseudonigrita* (1); *Sporopipes* (1). Process lacking, but lateral flange present.

Viduinae

The process in the widow birds is the same as that in the Ploceinae, but except for *Hypochera*, they lack the lateral flange.

Hypochera (1), lacking, flange present; *Steganura* (1), lacking, flange absent; *Vidua* (2), lacking, flange absent. Subfamilies of Ploceidae follow Tordoff (1954a), genera checked with Chapin (1917) and against the A.M.N.H. collection.

Sturnidae

The process is lacking (= fused) in almost all specimens of starlings examined. In a few specimens of *Sturnus*, a faint suture could be seen which suggests that the process is present in the immature and becomes fused with increasing age.

Acridotheres (2); *Creatophora* (1); *Lamprotornis* (4); *Mino* (2); *Onychognathus* (2); *Spreo* (8); *Sturnus* (11), hint of process in a few specimens. Process lacking. Checked with Amadon (1943).

Oriolidae

The process is lacking (= fused) in most specimens of this family. In a few specimens of *Oriolus*, a faint suture can be seen which indicates that the process is present in the immature and becomes fused with age.

Oriolus (23), present, but partly fused in five specimens, lacking in the rest; *Sphecotheres* (3), lacking. Checked against the A.M.N.H. collection.

Dicruridae

The process is lacking (= fused) in all specimens of drongos.

Dicrurus (39), lacking. Checked with Vaurie (1949).

Callaeidae

The process is lacking (= fused) in all specimens of this family.

Callaeas (1), lacking, heavy-billed form; *Neomorpha* (1, female), lacking, long, curved-billed species (the palatine process is not shown in the figure of the palate of the male [Garrod, 1872], which has a much shorter and stouter bill); *Philesturnus* (1), lacking, short slender bill. Checked with Stonor (1942).

Grallinidae

The process is lacking (= fused) in all specimens of *Corcorax* and *Grallina*, but present in *Struthidea*. This apparently represents a true difference between these genera which may be a reflection of the possible artificial nature of this family.

Corcorax (1), lacking; *Grallina* (8), lacking; *Struthidea* (4), present, lying along the palatine. Checked with Amadon (1950b).

Artamidae

The process is lacking (= fused) in this broad-billed, swallow-like genus, but in some specimens there is an indication that the process has fused with the palatine.

Artamus (7), lacking, but a faint indication in a few specimens. Checked with Mayr and Amadon (1951).

Cracticidae

The process is lacking (= fused) in all specimens examined in this family.

Cracticus (1); *Gymnorhina* (7); *Strepera* (3). Process lacking. Checked with Amadon (1951).

Ptilonorhynchidae

The process is lacking (= fused) in almost all specimens of the bowerbirds. Its presence in one specimen of *Ailuroedus* indicates that the process has fused to the palatine and that any variation in fusion is age variation.

Ailuroedus (5), present in one specimen; *Chlamydera* (2); *Ptilonorhynchus* (9); *Xanthomelus* (1). Process lacking. Checked against the A.M.N.H. collections.

Paradisaeidae

The process varies greatly in the birds of paradise. In most genera, it is lacking or heavily fused to the palatine. In a few genera, such as *Manucodia*, a quite distinct process is present in some specimens. In

Paradisaea (Figs. 28G, 28H, and 28I), the anterior connection between the process and the main body of the premaxilla begins to degenerate until only an isolated splint of bone remains. How much of the variation is true difference between genera is not known, but it is evident that a large amount of the observed variation is age.

Astrapia (3), lacking; *Cicinnurus* (6), lacking, a hint of the process in one specimen; *Craspedophora* (1), process partly fused; *Diphyllodes* (8), lacking; *Epimachus* (2), partly fused; *Lophorina* (6), partly fused to completely fused; *Loria* (1), lacking; *Manucodia* (5), present in two specimens, lacking in the others; *Paradisaea* (25), present in 23 specimens, degree of fusion varies, lacking in the other two; *Parotia* (5), partly fused to completely fused; *Phonygammus* (2) slightly fused; *Ptiloris* (1) partly fused; *Seleucides* (5), lacking; *Semioptera* (1), lacking. Checked with Mayr (MS for Peters' Check-list).

Corvidae

The process is lacking (= fused) in the adult crow; the observed variation in the degree of fusion is most likely due to age.

Calocitta (1); *Corvus* (34); *Crypsirina* (2); *Cyanocitta* (13), faint indication of a process in one specimen; *Cyanocorax* (10); *Garrulus* (2); *Kitta* (10); *Nucifraga* (3); *Perisoreus* (6); *Pica* (3); *Ptilostomus* (4); *Pyrrhocorax* (1). Process lacking. Checked with Amadon (1944).

EVOLUTION OF THE PALATINE PROCESS OF THE PREMAXILLA

The discussion of the evolution of the palatine process will, by necessity, be divided into two parts: (a) the general evolutionary principles involved; and (b) the evolutionary pathways traversed by the process (Fig. 29). I am interested here in determining how the palatine process has evolved — how it has changed from one condition to another — not in its actual phylogeny. It is, nevertheless, necessary to consider certain questions that are closely associated with problems of phylogeny, namely whether independent origin plus parallel evolution and reversal of evolution have played important roles in the evolutionary history of the palatine process. Throughout the discussion, the palatine process will be considered as a morphological structure independent of taxonomy, but it will always be integrated with the other structures of the character complex to which it belongs. These evolutionary conclusions are, of course, speculative with the weakest link in the chain of evidence being the functional conclusions. If future empirical studies on the function of the jaw mechanism in birds prove the functional deductions to be wrong, then these evolutionary conclusions also may well be wrong.

Evolutionary principles. A discussion of some basic evolutionary principles may seem to be out of place in this paper and even to be totally unnecessary. Yet in recent papers on avian anatomy and classification, there is a distressing lack of understanding and appreciation of evolutionary principles underlying morphological change. Mayr (1955, 1958) alludes to this problem and discusses some of the basic principles. The reader should consult these papers and the general treatises on major evolutionary change, such as Sewertzoff (1931), Simpson (1953), and Remane (1956), for a more complete coverage of this topic. Yet no single book or paper includes a discussion of all of the principles pertinent to the evolution of the palatine process. These principles will, therefore, be discussed to avoid any possible confusion in their meaning and use in the present paper. I shall restrict my remarks to the evolution of single characters and shall omit those principles, such as "mosaic evolution" and "key innovations," which apply to the evolution of species or groups.

a) Genetic potential: The members of a taxonomic group are basically similar in their genetic compositions which tend to change in a similar fashion. The similarity of the genetic composition and change depends upon the degree of relationship; the closer the relationship, the closer is the degree of genetic potential. This bipartite principle is one of the most important underlying the evolution of both single structures and taxonomic groups — in fact, it is basic to many other evolutionary concepts, including those to be discussed below — yet it is one of the least understood and appreciated concepts of evolution. Although brief, one of the best discussions of this concept can be found in Mayr and Vaurie (1948, p. 246) who conclude that: "Parallelism in evolution must be accounted for by such basic similarity of the germ plasm." Simpson (1953, pp. 348-349) alludes to this principle when he considers the problem of how related groups can acquire the same adaptation independently (i.e., the development of the mammalian jaw articulation in five different lines of therapsid reptiles). Again, Amadon (1956, pp. 15-16) suggests that some of the parallelism in the starlings has been facilitated by the genetic potential of this family.

The evidence supporting the concept of genetic potential is relatively simple and well known to most biologists. First, if there is a direct correlation between the genotype and the phenotype, then a group of related and structually similar forms would have to be similar genetically. This statement should be

reversed to read that a group of related and genetically similar forms would be similar in their phenotypical expression. However, since the genetics of most groups has not yet been worked out, we must use the more awkward converse. Second, it is well known that, although the occurrence of gene mutations is random, their direction is not random. A gene can mutate only to one of the several alleles found at that chromosomal site; the limitation is most probably imposed by the physical and chemical structure of the gene. Third, the mutant gene must act in harmony with the rest of the genotype if it is to have a selective advantage. Therefore, one can conclude that all of the Passeres are similar genetically and that a structure could change only in a rather limited number of ways. The palatine process of the premaxilla would, then, have a similar genetic basis in all of the Passeres and could change, both genetically and phenotypically, in a limited number of ways.

b) Developmental potential: Many structures are present at some time during development and disappear as visible structures in the adult, a phenomenon especially characteristic of the avian skeleton. Although these structures are "absent" in the adult, they must be regarded as being present in the species because their genetic basis is present and they appear in every generation in the developing animal. Why these structures are present only in the embryo — whether they have a role in development, or are the remnants of degenerating structures — is a most important question, but it is not pertinent to this study. The important thing is that the potential for the structure is present and that the structure could be restored or retained in the adult whenever selection would demand it. The evolution of a structure involving developmental potential may exhibit certain features which are more apparent than real. First, the sudden appearance of the structure may appear to be the result of a single large mutation and second, this mutation may appear to have occurred independently in several groups. Neither of these are correct. The structure, along with its genetical basis, is already present in the embryo and can be retained in the adult by inhibiting or suppressing the factors that cause its normal breakdown and/or disappearance. In the case of an osteological feature, the fusion of a bony process to another bone or its breakdown can be prevented if this process becomes the point of attachment of a muscle or a ligament. This is exactly what has happened in the evolution of the free palatine process. The process is present in all Passeres although it is absent as a

visible structure in the adult, but can "appear" in any family as a free palatine process if part of the M. pterygoideus takes origin from it.

e) Preadaptation: A preadapted structure is one whose form will allow it to assume a new function whenever need for that function should arise (Bock, 1959). The new function does not have to be related in any way to the original function of the preadapted structure. Its position along the palatine and the fact that it fuses to that bone relatively late in ontogeny preadapts the palatine process for the function as the origin for part of the M. pterygoideus as seen in the cardinals and several other families of passerine birds.

d) Multiple pathways of evolution: The same selection force acting on several groups of animals may elicit different adaptive responses depending upon the genotypic and phenotypic differences between these groups. These different adaptive responses would be the multiple pathways of adaptation or evolution. The basis for multiple pathways lies in the fact that there are usually several ways to achieve the same functional goal (see Simpson, 1953, pp. 179-181; and Bock, 1959). For example, at least two different methods for cracking seeds have evolved in the Passeres and each has its own special anatomical modifications including the structure of the palatine process of the premaxilla. Within this primary dichotomy of multiple pathways for seed-cracking, are secondary and probably even tertiary or lower levels of multiple pathways. If, for instance, a passerine bird has "chosen" the nutcracker method of seed-cracking, then there are a number of different ways of evolving the necessary adaptations, e.g., differential development of the several adductor and protractor muscles. The most important consequence of multiple pathways for the functional anatomist and the evolutionist is that morphological differences between the adaptations for the same function are non-functional and hence non-adaptive in terms of that particular function. Only differences between the structure in the ancestral and descendent species are functional and thus adaptive. Therefore, one cannot assume that all of the morphological differences between contemporary groups are adaptive differences. It must be emphasized, however, at this point, that multiple pathways can be discussed in terms of only one function, or in terms of only one selection force. The differences between the adaptive responses for one selection force may be adaptive in terms of other functions. Thus one condition may evolve to

another under the influence of these other selection forces. For example, although the differences between the adaptive responses — the nutcracker method and the vise method — for seed cracking in the Passeres are non-functional in terms of seed cracking, they are probably functional and adaptive in terms of insect catching. Thus the "vise structure" could change to the "nutcracker structure" and vice versa under the influence of selection forces associated with insect eating, but could not change under the influence of the selection force associated with seed cracking.

e) Independent origin and parallel evolution: These two evolutionary principles are independent in that one does not depend upon the other; however, because both are dependent upon the principle of genetic potential and because they frequently occur together, they are best discussed together. The term "independent origin" refers to the separate evolutionary origin of the same structure in different taxonomic groups, as for example the free palatine process in the flycatchers and the cardinals. This may be the result of *de novo* appearance of the structure because of similar genetical changes or it may be the retention of an embryological structure in the adult. Separation of these possibilities is impossible without detailed genetical and embryological investigations. "Parallel evolution" is similar evolution of a structure in different taxonomic groups, i.e., the structure undergoes the same series of changes. Clearly then, if the families of passerine birds have a basically similar genetical potential for a certain structure, that structure could arise independently and evolve in a parallel fashion if the same selection forces acted on the members of several families. Yet structures that have arisen independently do not have to undergo a subsequent period of parallel evolution and vice versa. Many examples of independent origin and of parallel evolution of the palatine process can be cited. Some notable ones could be the free palatine process in the cardinals. *Furnarius* and some of the tyrant-flycatchers, and the lateral flange in the carduelines, the ploceids, *Oryzoborus* and *Psittirostra*.

f) Convergence: Convergence occurs when formally dissimilar structures or structures in unrelated taxonomic groups become similar to one another. There is no sharp break between parallelism and convergence, and indeed some workers do not distinguish between the two concepts (see, however, Haas and Simpson, 1946, for a discussion of this problem). However, as there are several important differences between typical convergence and typical parallelism, I shall distinguish between them.

Cases of convergence in the palatine process are somewhat difficult to separate from parallelism because we know so little about the relationships of the passerine families. One example may be the evolution of the lateral flange in the carduelines and the ploceids if these groups are unrelated.

g) Reversal: Reversal is evolutionary change of a structure to a condition that is similar to the primitive or original structure. The sequence would be primitive — specialized — secondarily primitive. The question of whether reverse evolution means an exact backwards change involving the same steps and genetic changes is a moot if not a ridiculous problem. Most likely, reversal does not involve the same genetical changes, but this is of little importance. The important consequence of reversal is that a secondarily primitive structure frequently cannot be distinguished morphologically from an originally primitive structure! These morphologically similar, but evolutionary-wise different conditions usually can be separated from one another only after the phylogeny of the taxonomic groups has been determined. Reversal in the evolution of the palatine process had probably occurred many times, as for example, when an insectivorous group has evolved from a heavy-billed group. An example may be the evolution of the Drepaniidae from the Carduelinae with the loss of the lateral flange in the thin-billed members of the Hawaiian honey-creepers.

The most important feature of these several evolutionary phenomena, especially independent origin, convergence and reversal, is the frequency of their occurrence. If they were of rare occurrence during the evolution of a taxonomic group, then they would be of only minor importance. As their frequency increases, so does their importance in evolutionary and taxonomic studies as well as the difficulty in untangling the phylogeny of a group, but this increase in importance and difficulty is a rapid geometric increase. It is my belief that these phenomena were of common occurrence during the evolution of birds because birds share a very similar genetic potential. This appears to be especially true in the Passeres in view of their great similarity in structure. It is difficult, however, to cite indisputable examples of these phenomena in the case of the palatine process. The problem stems from the fact that we know so little about the phylogeny of the Passeres that we can never be certain, in many cases, whether similarity in the palatine processes of two families is the result of common ancestry, parallelism or convergence. Nor can we determine at this time the frequency of independent

origin and reversal. It is always better to be cautious in taxonomic studies, hence I shall stress the need to consider these phenomena at all times.

Evolutionary history of the palatine process.

a) Primitive form: The primitive condition of the palatine process of the premaxilla is that of the process lying along the lateral edge of the palatine and more or less fused with that bone — the normal condition of the palatine process as seen in the crow or the white-throated sparrow. It is impossible to determine whether the palatine process of the premaxilla was completely or only partly fused with the prepalatine process of the palatine in the ancestral passerine bird, but this is of little importance. Change from an incompletely fused process to a completely fused one or vice versa is exceedingly simple and has probably occurred repeatedly during the evolution of the Passeres. Two bits of evidence support the conclusion that the normal palatine process is the primitive condition. First, this is the condition found in most passerine birds as well as in most other birds. If the normal palatine process was not the original condition in the Passeres, one would have some difficulty explaining its present-day distribution in the passerine families. Second, all other conditions of the palatine process in the passerines appear to be specializations for some particular mode of feeding. This is certainly true for the free palatine process and the lateral flange on the prepalatine process.

b) Selection forces: The factor most frequenly omitted from discussions of the evolution of a structure is the set of selection forces acting on that structure. In the case of the palatine process, the primary function and hence the primary selection force is insurance of a firm connection between the palate and the upper jaw. This selection force may not have been responsible for the origin of the palatine process which probably took place some time in the early history of the birds, if not earlier. However, this selection force is responsible for the maintenance of the palatine process in birds and for some of the variation in the degree of fusion with the prepalatine process. All modifications of the palatine process in the Passeres must always fulfill the demands of this primary selection force. The secondary functions and hence the secondary selection forces acting on the palatine process are independent of each other, and indeed they apparently cannot act together in harmony. One of the secondary selection forces is associated with the vise method of cracking seeds and selects for the fusion of the palatine process

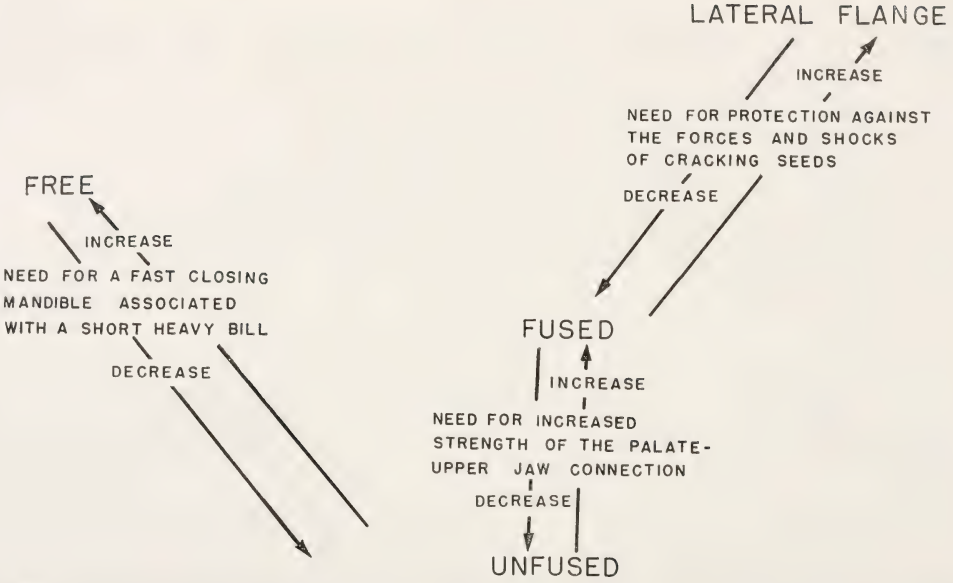

Figure 29. Dendrogram showing the evolutionary pathways in the evolution of the palatine process. The selection forces bisect the lines leading from one condition to another. See the text for further explanation.

with the prepalatine process and the development of a lateral flange at the site of fusion. The other secondary selection force is associated with a fast closing mandible during the early phases of closing the bill and selects for a free palatine process from which a portion of the M. pterygoideus originates.

c) Maintenance of the palatine process: During most of the evolution of the Passeres, there was little or no change in the structure of the palatine process. Slight changes in the strength of the primary selection force had no doubt occurred which could account for some of the variation in the degree of fusion between the palatine process and the palatine, as for example, in the Dendrocolaptidae and the Pipridae. Parallelism in the amount of fusion of the palatine process or in its degeneration as an isolated splint of bone lying along the palatine are probably common, as are reversals in the trends of fusion or breakdown. It is impossible to determine whether the normal condition of the palatine process in any group of passerine birds is originally primitive or secondarily primitive or even, as will be shown later, if the group had passed through an earlier stage having a more specialized type of palatine process.

d) Evolution of the free palatine process: The evolution of the free condition of the palatine process is dependent upon changes in the M. pterygoideus ventralis lateralis. This muscle becomes larger in some passerine birds with the lateral superficial fibers extending forward along the palatine. It has been shown that the forward extension of these fibers has several important functional consequences in addition to the increased strength of the muscle. These fibers would be longer than all other fibers of this muscle; hence it would appear reasonable to suggest that their action is faster and over a longer distance than the shorter fibers of the M. p. ventralis lateralis. It has been pointed out above that the insertion of these superficial fibers is such that their main function is to raise the mandible during the early phases of closing the bill. This is a rapid, but not a very powerful closing of the bill. Once the origin of the superficial fibers reaches the anterior end of the palate, the palatine process can assume the role of the point of origin. The detailed steps leading up to this are outlined below.

The tendon of this superficial bundle runs forward along the palatine to attach somewhere along that bone or at the junction between the palatine and the premaxilla in the more advanced forms. This tendon is closely associated with the periosteum of the palatine, especially where the tendon takes

origin from the palatine. In the more advanced forms, the tendon takes origin from the periosteum of the palatine process. As the superficial bundle of the M. pterygoideus increases in size, its tendon shifts away from its original position along the palatine until it is free of the palatine for most of its length. Finally, the tendon meets the palatine bone at a slight angle. At this time, the tendon usually originates from the fused or the partly fused palatine process, although it has not yet influenced the position or the fusion of the palatine process which is still only under the control of the primary selection force. But, as has been pointed out above, the palatine process fuses to the palatine bone relatively late in ontogeny. Thus, if the tendon of the superficial bundle originates on it and if this tendon approaches the palate at a slight angle, then the distal end of the palatine process would be "pulled" away from its original position along the palatine to a new position in the space between the palate and the jugal bar. The distal end of the palatine process, then, could not fuse to the prepalatine process. However, the anterior part of the process still fuses with the palatine, which apparently fulfills the demands of the primary selection force. In its new position, the palatine process would be free of the palatine and at a slight angle as well as a little ventral to it. The process would, thus, lie exactly in line with the longitudinal axis of the superficial bundle of the M. pterygoideus and hence would be in the most effective position as the point of origin for that muscle. Once the palatine process is free of the palate, some ossification of the tendon may occur, thereby lengthening the process. Proof of this point is exceedingly difficult to obtain because ossified tendons are practically indistinguishable from normal bone, both macroscopically and microscopically. However, this is a minor point with no direct bearing on the evolution of the free palatine process.

The development of the superficial bundle of the M. p. ventralis lateralis is an exceedingly simple evolutionary change and has probably occurred independently many times during the evolution of the Passeres. Here is the basis for the independent origin, parallel evolution and even convergence of a free palatine process. The normal palatine process, no matter whether it is incompletely or completely fused to the prepalatine process, is preadapted to evolve into the free process with the appearance of the selection forces favoring this condition (i.e., the development of the superficial bundle of the M. pterygoideus). The appearance of a free process in a group that does not have a

visible palatine process in the adult is facilitated by the genetic and developmental potential alluded to above.

Loss of the free palatine process and reverse evolution back to the normal condition will occur whenever the M. pterygoideus changes back to its original condition, i.e., by losing the superficial bundle of fibers. The loss of this separate bundle is not associated with decrease in the strength of the bite, but would occur if the bird no longer needed a fast closing bill or had developed a more efficient way to close the bill rapidly, as, for example, by lengthening the bill and palate which automatically lengthens the M. pterygoideus. In fact, the only birds with a free palatine process or with tendencies toward this condition are those which must combine a short bill with rapid closing. If a group had lost the free palatine process and returned to the normal condition, there would be no way of distinguishing the secondary normal condition from the primary or primitive normal condition. Thus we cannot determine which of the tanagers possessing a normal palatine process has evolved from ancestors possessing a free palatine process. Nor can we determine whether or not the ancestors of the emberizine finches had a free palatine process. Such determinations must wait until the true phylogeny of these groups has been established.

e) Evolution of the lateral flange: The evolution of the lateral flange is far simpler than the evolution of the free palatine process. Most, if not all, birds have a membrane stretching between the prepalatine process and the jugal bar or the lateral edge of the upper jaw. This membrane is part of the lining of the roof of the mouth. Ossification of this membrane is the easiest and probably the most efficient way of achieving additional protection in this region of the skull against the shocks that may accompany cracking seeds by means of the vise method. Such ossification would result in an automatic fusion of the palatine process with the palatine if it was not already fused, and in the subsequent development of the lateral flange as seen in the cardueline and the ploceid finches. Additional protection such as the development of overlying pads of rhamphotheca can evolve after the development of the lateral flanges. I need scarcely point out the ease with which the lateral flange could arise independently in different groups and evolve in a parallel fashion or converge depending upon how distantly related the groups were. Also, reversal can occur when the selection force for protection against the forces and shocks of feeding is no longer in existence. The secondary normal palatine process, such

as may occur in some of the thin-billed Drepaniidae, is indistinguishable from the primitive normal palatine process.

TAXONOMIC VALUE OF THE PALATINE PROCESS OF THE PREMAXILLA

With the aid of the information on the evolution of the palatine process gathered in the preceding section, we can proceed to the evaluation of its taxonomic significance — this being the ultimate aim of any study of a taxonomic character. The taxonomic value of the palatine process in relating families of passerine birds will be evaluated first, followed by a discussion of the relationships of certain families and genera based on the evidence of the palatine process and, in part, the jaw muscles. I wish to emphasize that these discussions on the relationships of the various families and genera are only suggestions based on the available data; they are not hard and fast opinions or conclusions on the affinities of these groups. Here again, I might reiterate my earlier statement that it is my belief that we do not have and probably will not have for many years, the necessary body of evidence on which to base conclusions on the relationships within the Passeres.

Taxonomic value. The taxonomic value of a structure depends, as has been mentioned above, upon the nature of the controlling selection forces. If these selection forces have a tight control over the structure and if they have arisen repeatedly and changed direction often during the evolution of the group, then that structure would have very little taxonomic value in that group. One could argue about the degree of control on the palatine process by the several selection forces guiding its evolution, but it is reasonable to assume that these selection forces exert a fairly tight control on the palatine process. There is little question, however, about the fact that the several controlling selection forces have arisen repeatedly and have reversed their direction numerous times during the evolution of the perching birds. Therefore, I would conclude that the palatine process of the premaxilla has *little or no* value in showing relationships between families of passerine birds or in placing problem genera into the correct family. Here, I must disagree with Tordoff, who concluded (1954a, p. 33) that the palatine process provides a good clue to relationships in the New World nine-primaried oscines. The taxonomic changes advocated by Tordoff are consequently not justified on his evidence and should not be accepted unless supported by other evidence. A detailed discussion of these changes will be given below.

The Passeres and the New World nine-primaried oscines. The palatine process of the premaxilla does not offer any clues which might help solve the problem of the relationship of the Passeres to other orders, or the problem of the major groupings within the Passeres. I should mention again that the results of this study neither support nor refute any of the arrangements proposed in recent years of the Passeres or of the Oscines. There are, however, parts of each system that are not in agreement with the available evidence provided by the palatine process and the jaw muscles. For example, the separation of the Fringillidae (Carduelinae + *Fringilla*) from the Emberizinae in both Mayr and Greenway's, and Amadon's lists does not agree with the similarity in the configuration of the jaw muscles of these groups. The separation of some of the New World nine-primaried families in Wetmore's arrangement does not appear to be justified in view of the great similarity of these families. In fact, all of the available morphological evidence indicates that the nine-primaried oscines are a monophyletic group. The structure of the palatine process of the premaxilla, although it does not provide any strong proof for a monophyletic origin of the nine-primaried group, at least does not argue against it. However, the relationships within this assemblage are exceedingly complex and for all practical purposes, are completely unknown. The probable ancestral group and the directions of evolution within the group are anyone's guess. In fact, the family limits cannot be defined with any degree of certainty; hence many problem genera cannot be allocated to the proper family or subfamily. Although much work has been done toward the clarification of the relationships between the nine-primaried families, much more must be done before the problem is solved; however, it is hoped that in the future, more attention will be paid to the group as a whole and not to whether this family is allied to that family, or where a certain problem genus should be placed.

Vireonidae. The vireos are, in the opinion of many workers including myself, the most likely representatives of the ancestral nine-primaried stock. The reasons for this choice are negative rather than positive, namely that the vireos are relatively generalized insect-eaters while most of the other nine-primaried families are apparently specialized in one way or another. Rejection of Tordoff's hypothesis that the free palatine process as found in the cardinals is the primitive condition eliminates one of the serious objections to the vireos being the ancestral nine-primaried oscines. The vireos have a normal palatine process, a relatively

unspecialized set of jaw muscles, and a tenth primary (only some species), all of which support the hypothesis that the vireos represent the ancestral nine-primaried stock. Yet, this evidence is not very conclusive and much more is needed to verify this hypothesis.

Vireolanius and *Cyclarhis* have been included in the Vireonidae. They appear to be heavy-billed vireos with a more heavily fused palatine process. It should be pointed out, however, that we do not have a single, thorough, study evaluating the morphological differences between these genera and the vireos.

Parulidae. The arguments for the origin of the wood-warblers either from the vireos (Beecher, 1953, p. 307) or from the emberizine finches (Tordoff, 1954a, 1954b, p. 278) are based on rather weak evidence. Tordoff's argument stems from his insistence that the free palatine process is the primitive condition and that evolution proceeded mainly or only in the direction of reduction and loss of the palatine process. If the wood-warblers arose from the vireos, which is not an unlikely hypothesis, then Beecher may be correct in stating that the pinnate muscles of the warblers (as for example, the M. pseudotemporalis superficialis which serves to raise the mandible during the early phases of closing the bill) may have given them an advantage over the vireos which have only parallel-fibered muscles. Pinnate muscles do not develop only in response to selection for increased strength; they may have other functions, perhaps speed, which we do not suspect and thus could develop in response to selection for these functions. However, it must be emphasized that there is very little evidence available that may shed light on the origin and affinities of the Parulidae.

Icteridae. Again the arguments advanced by Beecher (1951a, 1953) and Tordoff (1954a) for the origin of the Icteridae from the Emberizinae are inconclusive; the necessary evidence is simply not available. Beecher's statement that the cowbirds, *Molothrus,* represent the ancestral stock of the icterids is pure speculation. The dickcissel, *Spiza,* will be discussed below with the cardinals.

Coerebinae. The New World honey-creepers (Coerebinae) provide an excellent example of the hodgepodge nature so characteristic of the nine-primaried families. Beecher (1951b) is probably completely correct in pointing out the polyphyletic nature of the honey-creepers, but I am not convinced that he has solved the convergence problem and clarified the affinities of the coerebid genera. It is likely that most of the honey-creepers have evolved

from the wood-warblers or from the tanagers, but whether there are two clear-cut groups, the Coerebini (nectar-feeding warblers) and the Dacnini (nectar-feeding tanagers), is another question. Beecher's interpretations of the similarities in the jaw muscles between the Coerebini and the warblers and between the Dacnini and the tanagers are not convincing (see above, p. 400, for a general discussion of Beecher's work). Of the other evidence — the horny palate relief, plumage pattern and differences in the manner of feeding — presented by Beecher, only the nature of the ridges on the horny palate appear to have any value in showing affinities. However since I have not studied this feature, I do not feel qualified to evaluate it. It is interesting that Tordoff (1954a, pp. 30-31) has found the palatine process to be absent in the Coerebini, as in the warblers, but present and more or less fused with the palatine in the Dacnini, as in the tanagers, thereby supporting Beecher's earlier conclusion. I have found much variation in the degree of fusion between the palatine process and the palatine bone in the honey-creepers, but was not able to ascertain any differences in the degree of fusion between the genera assigned to the Coerebini and those assigned to the Dacnini by Beecher. In view of this inconclusive evidence, I would agree with Mayr and Greenway (1956) who recognize the old group "Coerebinae" even though they realize that it is of polyphyletic origin. The only alternative solution at the present time is to list the genera of honey-creepers as *genera incertae sedis*. However, since both alternatives accomplish the same end result, it is best to retain the old "Coerebinae" until we have discovered the true affinities of its genera.

Cardinalinae and Tanagrinae. The cardinals and the tanagers are so similar to one another in many respects and seemingly grade so imperceptibly into one another that they are best discussed together. Beecher (1953) and Tordoff (1954a) agree that the cardinals are related to the tanagers, but disagree on the direction of evolution. Nelson (1954) agrees that the two groups are related on the basis of similarity in the pneumatic fossa of the humerus, but believes that these families are not related to the Emberizinae (see Berger, 1957, pp. 266-267, for a discussion of the pneumatic fossa of the humerus). There cannot be any question that the cardinals and the tanagers are very similar morphologically, but I doubt that the evidence advanced by these authors proves that they are closely related within the nine-primaried assemblage. Nor can the evidence be used to distinguish between the cardinals and the tanagers, or between

either or both families and the emberizine finches. Mayr (1955, p. 34) pointed out that the direction of evolution in the nine-primaried oscines, and especialy in these three families, is in doubt. This is still true. It seems certain that the free palatine process of the cardinals is not the primitive condition in the New World nine-primaried oscines, but we cannot tell whether the emberizine finches gave rise to the tanagers or vice versa, or whether the cardinals gave rise to the tanagers or vice versa, or whether these groups are more distantly related. We cannot even be sure that the cardinals and the tanagers are good taxonomic groups. For these reasons, I do not see the point of worrying about the correct position of the numerous problem genera — especialy those from tropical regions — of the nine-primaried finches. What difference does it make whether *Saltator* is a tanager or a cardinal, or whether *Chlorospingus* and *Orcothraupis* are tanagers or emberizine finches when we have no idea of the limits of the familial groups.

One genus, *Spiza*, must be discussed because of the importance placed on it by Tordoff. In both of his papers (1954a, 1954b, p. 218), Tordoff placed *Spiza* in the Cardinalinae and claimed that it represents the ancestral fringillid and consequently the ancestral nine-primaried stem stock better than any other living genus. This opinion is based on his belief that the free palatine process is primitive; his other reasons supporting this opinion are incidental. On the other hand, Beecher (1951a, 1953, p. 309) claimed that *Spiza* is an icterid on the basis of the configuration of the jaw muscles, although he did not figure these muscles in either paper. There is no question about the structure of the palatine process in the dickcissel; it is free as in the cardinals, but this is far from proof that it is a member of the Cardinalinae. Unfortunately, I have not been able to dissect the jaw muscles of the dickcissel, but I would be most surprised if a superficial bundle of the M. pterygoideus ventralis lateralis did not originate from the free palatine process. It is of interest that in some icterids, such as the grackle, the M. p. ventralis lateralis sends a lateral tendon forward for a short distance along the palatine. This indicates that the potential for developing a separate superficial bundle of the M. pterygoideus and a free palatine process may be present in the icterids. Most of the other evidence cited by both Tordoff and Beecher is likewise inconclusive. For example, the similarity in color pattern between the dickcissel and the meadowlark may well be convergence because of their living in the same habitat, as has been pointed out by Friedmann

(1946). New and different evidence is needed before the affinities of *Spiza* are clarified.

The swallow-tanager, *Tersina*, scarcely deserves a separate discussion. In the structure of the palatine process, this genus appears to be a tanager, but whether it should be placed in that group or in a group of its own is another problem. It is interesting that the true swallows usually have an unfused and quite distinct palatine process. Although I have not dissected the jaw muscles of these groups (the one swallow I examined was a damaged specimen), I would suspect that a part of the M. pterygoideus took origin from the palatine process and had the function of raising the mandible rapidly, as in the cardinals and the tanagers. I also suspect that such an arrangement of the M. pterygoideus will be found in some of the tyrant-flycatchers.

Fringillidae and Emberizinae. The Fringillidae of older authors are, with little doubt, one of the most controversial families in the nine-primaried complex. Most of the recent arguments about relationships in the nine-primaried oscines center about the Fringillidae or start with them. This family according to the older classifications, e.g., Wetmore, is composed of the Emberizinae, the Cardinalinae and the Fringillinae (including the carduelinе finches). Many recent workers suspected, however, that this family is polyphyletic in origin and have set out to uncover the true affinities of the several subfamilies. The conclusions of the various authors differ radically, but they need not be summed up here. The only one that will be considered is Tordoff's conclusion that the carduelinе finches (excluding *Fringilla*) do not belong to the nine-primaried group, but are related to the ploceids. *Fringilla*, according to Tordoff, is a primitive emberizine finch. The only recent modification of Tordoff's conclusions has been that of Mayr, *et al.* (1956) who concluded that *Fringilla* is closely related to the carduelines. Because I believe that Tordoff's reasons for separating the carduelinе finches from the nine-primaried assemblage are baseless, it is necessary to re-examine the entire problem of the "Fringillidae." In doing so, I will use only the morphological evidence, especially that supplied by the cranial anatomy.

There seems to be little disagreement about the conclusion that the cardinals are closely related to the emberizine finches. If the cardinals are included in the "Fringillidae," then the tanagers will most likely also have to be included. However, in view of the inconclusive evidence pertaining to the affinities between the cardinals and the emberizine finches, this aspect of the

problem will be dropped and attention will be concentrated on the relationships between the emberizine finches and the cardueliines plus *Fringilla*.

Mayr, *et al.* (1956) have presented much evidence pointing to a close affinity between *Fringilla* and the cardueline finches; one of the most serious disagreements was the unfused palatine process in *Fringilla* as compared to the fused process and the lateral flange in the cardueliines. The results of the present study have shown that the presence of an unfused palatine process in *Fringilla* and its apparent absence in the cardueliines does not necessarily mean that the two groups are unrelated, as supposed by Tordoff. Although *Fringilla* does not possess a lateral flange, its jaw muscles are almost identical to those in the cardueline finches as has been reported earlier by Fiedler (1951) and Beecher (1953). The most distinctive feature of the cardueline jaw musculature is the enlarged medial portion of the M. pseudotemporalis superficialis. *Fringilla* agrees completely with the cardueliines in this feature. The major difference between the jaw muscles of the two groups is the poorly developed M. adductor mandibulae in *Fringilla* which is similar to that found in the emberizine finches (see Fiedler, 1951, p. 242). This muscle is highly developed in the cardueliines with two parts expanding over the side of the skull. In addition, some of the emberizine finches, e.g., the fox sparrow, tend toward the cardueline finches in the structure of the M. pseudotemporalis superficialis and the M. pterygoideus. Thus in several aspects of the bony palate and the jaw musculature, *Fringilla* is intermediate between the emberizine and the cardueline finches, but it is closer to the cardueliines. On the other hand, none of the ploceid or estrildid finches, to my knowledge, tend toward the cardueline arrangement of the jaw muscles, especially in the very distinctive condition of the M. pseudotemporalis superficialis. I must emphasize, however, that I have dissected only the house sparrow (*Passer*) and the heavy-billed *Coliuspasser* and examined Beecher's plates of the jaw muscles in the ploceid and estrildid finches so that my sample of these finches is quite small.

Although no definite conclusions on the relationships between the fringillid, emberizid and ploceid finches can be based on the available evidence from the cranial morphology, several hypotheses may be advanced. I cannot see any indications of a relationship between the cardueliines plus *Fringilla* and the ploceids or the estrildids, as advanced by Tordoff. Because of the intermediate position of *Fringilla* in many features of the cranial

anatomy, it does seem reasonable to suggest that the emberizine finches gave rise to the carduelines through a *Fringilla*-like group. The cardueline radiation could have eliminated an earlier *Fringilla* radiation except for *Fringilla* itself. If this hypothesis is correct, then the Fringillidae of Wetmore is a monophyletic group and the similarity between the Carduelinae and the Estrildidae and the Ploceidae in the structure of the lateral flange would be convergence. It is entirely possible, however, that the carduelines plus *Fringilla* are related to the ploceids or the estrildids and that the similarity between the fringilline finches and the emberizines in the structure of the jaw muscles is due to convergence.

Drepaniidae. The origin of the Hawaiian honey-creepers remains a deep mystery even after many workers have devoted much time to this problem. One of the main reasons why the origin of the Drepaniidae has eluded ornithologists is because the structures so far studied were those which could never supply conclusive clues to their affinities. Although Drepaniidae constitute one of the best examples of adaptive radiation in feeding methods in the Passeres, the investigations of most workers on the origin of this group are based on characters associated with feeding methods. The present study of the palatine process has shed some light on this problem and I wish to offer the following ideas as a suggestion.

The group that gave rise to the Hawaiian honey-creepers had to have three characteristics. They had to be birds that wander in flocks, preferably erratically, over long distances, and breed at the place to which they have wandered. Of all the possible ancestral groups, the cardueline finches are the only ones that possess all three attributes. Here again, it must be pointed out that the objection to the carduelines as the ancestral drepaniids, presented by Tordoff, has been removed. It is quite possible that a cardueline finch or a member of its ancestral group had reached the Hawaiian Islands and gave rise to the Drepaniidae, a hypothesis already advanced by Sushkin (1929). The possession of a finch bill, even a heavy cardueline bill with its lateral flanges on the prepalatine process, does not present any problem for this hypothesis. The lateral flanges can be lost whenever the selection forces for them are eliminated or reversed. It is interesting that the bones of the palate and upper jaw of the heavy-billed genus *Psittirostra* are identical to those found in the large-billed carduelines. According to Beecher (1953, p. 311), the jaw muscles, including the expanded medial part of the M. pseudotemporalis

superficialis, of *Psittirostra* are almost identical to those of the cardueline finches. This suggested origin of the Drepaniidae is speculation and must be verified or rejected on additional evidence. I have offered it mainly to counteract the trend of thinking that the Hawaiian honey-creepers had to originate from a thin-billed member of the nine-primaried oscines.

CONCLUSIONS

A sharp distinction was made in the beginning of this paper between comparative studies of many characters in two or a few passerine families and comparative studies of a single character or character complex in the entire order Passeres, with the tacit, but clear implication that the former rarely led to conclusive taxonomic results. It is now necessary to evaluate the conclusions which may be gained in the latter type of study.

The first thing that probably comes to the mind of most readers is the highly speculative and inconclusive taxonomic results presented above. In fact, the only definitive conclusions were negative ones. These inconclusive results are scarcely surprising in view of the fact that they are based on the evidence supplied by a single character complex. Nevertheless, these are not very encouraging results for a taxonomic paper. Let us look, however, on the positive side of the ledger. This study has provided detailed knowledge of the structure and variation of the palatine process along with some information on its embryological origin and a fairly good idea of its functional significance. With this information, it was possible to gain a reasonably accurate picture of the evolution, although not of the actual phylogeny, of the palatine process. Such data, especially those on the evolution, are only rarely supplied by comparative studies of two families. Yet one can ask, what can be done with this information? If only a few inconclusive taxonomic results can be reached after such an extensive study as the present one, then why continue with these studies if one is primarily concerned with the classification of the perching birds? With comparative studies of families, we at least know how different these families are. Would it not be best to return to these studies?

The answer, or at least my answer, to the last question would be no. Still there is no reason to continue these extensive studies of single characters for the sake of the taxonomic deductions that may be reached in individual works. But then, why do taxonomic conclusions have to be offered at the end of every

taxonomic study? Is it not enough to present the data in such a way that they can be used to help formulate sound judgments of affinities when enough data have been gathered? With only a single study, such as the present one, very little if anything can be learned about the evolution and relationships of the Passeres. Perhaps a bit more can be learned with two or three studies. However, with several dozen such works, there would be a good chance of unraveling the entire evolutionary history of the recent Passeres. The evolution of the individual characters could be pieced together to form an overall evolution of the Passeres. Use of a large number of different characters will reduce the chance of error to an insignificant amount. This overall picture of the evolution of the Passeres will then serve as the basis for a classification of the order. It is my firm belief that a sound classification of the passerine birds can best be reached through a series of single character studies. This is a long and tedious task with relatively few rewards until the central problem is finally solved. But there are no short cuts to the goal, so that the sooner thorough analyses of single characters are begun, the sooner we will have a suitable classification of the Passeres.

SUMMARY

A comprehensive analysis of a single character — the palatine process of the premaxilla — in the Passeres is presented as a basis on which to judge the merits of the "single character study" approach to passerine classification.

The four major conditions — fused, unfused, free, and with a lateral flange — of the palatine process are described.

A history of the past studies is presented in which the origin of the erroneous term "palato-maxillary" for the palatine process is shown.

The embryology of the palatine process in birds possessing the process and in birds supposedly possessing the "palato-maxillary" is compared. It is shown that these terms refer to the same structure in the passerines and hence "palato-maxillary" should be dropped from use since it is the younger term.

The functional significance of the palatine process is discussed with two separate problems in mind. The first is the maintenance of the process in birds. It is shown that the primary function of the palatine process is insurance of a firm palate-upper jaw connection which is associated with the kinetic skull. The second problem concerns the modifications of the palatine

process in the finch-like Passeres. These modifications are associated with certain aspects of seed-eating. Therefore, it is necessary to investigate the correlation between the process and the M. pterygoideus (the only muscle attached to the palate), the different ways to increase the force of the bite and the methods by which the several groups of finches crack seeds. It is shown that the free palatine process serves as the point of origin for part of the M. pterygoideus and is associated with the nutcracker method of cracking seeds. This is an adaptation for a rapidly closing mandible. The lateral flange is associated with the vise method of cracking seeds, and is an adaptation for protecting the brain and sense organs from the forces and shocks that accompany the cracking of seeds.

Finally, the results of a survey of the palatine process in the Passeres are presented with a résumé of the types of inter- and intrafamilial variation.

The evolution of the palatine process is outlined with a short discussion of the several evolutionary principles that figure in its evolution. The normal condition of the palatine process — lying along the palatine and fused or unfused to it — is assumed to be primitive. Change from the fused to the unfused condition and vice versa has doubtless occurred repeatedly during the evolution of the Passeres. Evolution of the free process from the unfused process is under the control of selection forces for a fast-closing bill, while the evolution of the lateral flange is under the control of selection forces for protection of the braincase. These evolutionary changes can be reversed with a reversal of the selection forces. Apparently, the free process cannot evolve directly into the lateral flange; it must first pass through the normal condition.

It is concluded that the palatine process has little value in showing relationships between families of passerine birds. Some of the problems of relationships within the nine-primaried oscines are discussed, but no definite conclusions are reached.

Although individual studies of single characters, such as the present one, do not lead to definite taxonomic conclusions, it is suggested that comprehensive studies of single characters throughout the Passeres will eventually provide the best basis for understanding relationships within the order and it is urged that more studies of this type be undertaken.

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ABBREVIATIONS USED IN THE FIGURES

Muscles:

MAM = M. adductor mandibulae
MDM = M. depressor mandibulae
MPDL = M. pterygoideus dorsalis lateralis
MPDM = M. pterygoideus dorsalis medialis
MPQ = M. protractor quadrati
MPTP = M. pseudotemporalis profundus
MPTS = M. pseudotemporalis superficialis

Muscles:

"MRP" = "M. retractor palatini"
MPVL = M. pterygoideus ventralis lateralis
MPVM = M. pterygoideus ventralis medialis
T = tendon of the superficial bundle of the M. pterygoideus ventralis lateralis

Bones:

BT = basitemporal plate
DPM = dentary process of the premaxilla
IPP = interpalatine process of the palatine
JB = jugal bar
LF = lateral flange of the prepalatine process
M = maxilla
MP = maxillo-palatine
MPP = mediopalatine process of the palatine
MSP = medial shelf of the palatine
NFH = nasal-frontal hinge
P = palatine (except in figures 23 to 28)
PM = premaxilla
PP = prepalatine process of the palatine
PPM = palatine process of the premaxilla (in figures 23 to 28, abbreviated as P)
PT = pterygoid
Q = quadrate
TPP = transpalatine process of the palatine
V = vomer

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THE SNAKES OF ECUADOR

A Check List and Key

By James A. Peters

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The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 9 — *The Snakes of Ecuador. A Check List and Key.*

By James A. Peters

INTRODUCTION

As my work on the herpetofauna of Ecuador progressed, it became obvious that a complete key to the genera and species to be found in that country had to be prepared. Also, an adequate check list of the fauna including known and expected taxa was needed, for work on the geographical and ecological problems was halted until such a time as the actual fauna was better known. This check list and key to the snakes of Ecuador is, I hope, the first of a series to cover the entire reptilian and amphibian species of the country. In the course of its preparation, it has been necessary to make gestures in the direction of solution of several problems that were and still remain of considerable magnitude in South American herpetology. I have tried to avoid attacking these problems on the basis of artificial, political boundaries, particularly on the generic and familial level. The use of political units as the basis for analysis of a fauna is an expedient one, but it should not be extrapolated to form the basis of a taxonomic review or revision. If work is to be done on a particular genus, it should, if possible, cover the genus throughout its range, not just that genus within a political unit. Much of the difficulty encountered today in South American herpetology results from earlier use of this restricted approach.

METHODS

This check list has been drawn up with an eye toward making it of maximum usefulness to anyone interested in identifying a snake from Ecuador. It is, in fact, left in the same arrangement in which I have worked with it over the past ten years, and which I found most useful. The genera are arranged alphabetically throughout, rather than phylogenetically (for the phylogeny of Ecuadorian snakes, see page 493). The species are also arranged alphabetically within their genera. The phylogeny of many if not most South American snake genera is so poorly known that any attempt at an overall phylogenetic arrangement would be presumptuous, at best. Under each taxon I have included, first, a citation to the original description of that taxon plus its type locality and its holotype; second, citations for any taxon with its type locality in Ecuador that has been synonymized with the species, its type locality and its holotype; and third, as accurate

a statement of the entire range of the taxon as possible. I have made no changes in status of any taxon solely within the pages of this check list. Although no documentation as to the authority for changes of generic position has been presented in the species synonymy, this is deliberately omitted, and its absence is not to be construed to mean that the combination appearing here is a new one. On the contrary, there are no new combinations in this list, whatsoever. The generic position of every species has been previously documented in the literature, with one exception: I have followed Bogert's suggestion (*in litt.*) that *Synophis* and *Diaphorolepis* be considered distinct genera, and in this act anticipate his published documentation.

The presence in the keys of a genus or species name followed by an asterisk indicates that there is no valid record of the occurrence of that taxon in Ecuador, but that the likelihood of its being taken there in the future is sufficiently good that its presence should be anticipated. It should not be construed from this that I have been so perspicacious that I have successfully anticipated and included *all* likely new members of the fauna. Any specimen that does not fit in the key is not necessarily a representative of a species new to science, and must needs be checked against the considerable literature on South American snakes. This is particularly true of specimens from the Amazonian slope.

Under each species, the reference to the holotype in the species citation includes first an abbreviation of the name of the museum which acts as custodian for that specimen, and the catalogue number assigned to the specimen by the museum.

The abbreviations used are as follows:

ANSP — Academy of Natural Sciences, Philadelphia
BerM — Berlin Museum
BM — British Museum (Natural History)
CNHM — Chicago Natural History Museum
DroM — Drottningholm Museum
GothM — Gothenberg Museum
GottM — Göttingen Museum
HM — Hamburg Museum
IB — Instituto Butantan, São Paulo, Brazil
IdlS — Instituto de la Salle, Bogotá, Colombia
IRB — Institut Royale d'Histoire Naturelle de Belge, Brussels
JAP — James A. Peters Collection
LeyM — Leyden Museum
LunM — Lund Museum
MAF — Museum Adolphus Frederici

MCZ — Museum of Comparative Zoology, Harvard
MilM — Milan Museum
MonM — Monaco Museum
MPB — Musée des Pays-Bas
MunM — Munich Museum
MVZ — Museum of Vertebrate Zoology, Berkeley
PM — Museum National d'Histoire Naturelle de Paris
RMS — Royal Museum, Stockholm
Senck — Senckenberg Museum, Frankfort, Germany
SU — Natural History Museum, Stanford University, California
TurM — Turin Museum, Italy
UMMZ — University of Michigan Museum of Zoology, Ann Arbor
UNZM — University of Naples Zoological Museum, Italy
USNM — United States National Museum, Washington, D. C.
VM — Vienna Museum
ZIU — Zoological Institute, Uppsala, Sweden
ZSBS — Zoologischen Sammlung des Bayerischen Staates, Munich

CLASSIFICATION

As pointed out elsewhere, the arrangement in the check list is entirely alphabetical. This facilitates use of the list, but tells nothing about the phylogenetic relationships of the genera included. I have listed below the eight families of snakes that are represented in the Ecuadorian fauna, with the genera placed in their proper categories. I have not recognized the Boiginae, for the polyphyletic nature of this supposed subfamily of the Colubridae is obvious. I have followed Dunn and Dowling (1957:260) in assigning *Nothopsis* to the Colubrinae rather than to a subfamily of its own.

Typhlopidae
  Typhlopinae
    Typhlops
  Anomalepinae
    Anomalepis, Liotyphlops
Leptotyphlopidae
  Leptotyphlops
Boidae
  Boinae
    Boa, Corallus, Epicrates, Eunectes
  Tropidophinae
    Trachyboa, Tropidophis
Anilidae
  Anilinae
    Anilius

Colubridae
Colubrinae
Atractus, Chironius, Clelia, Coniophanes, Dendrophidion, Diaphorolepis, Drepanoides, Dryadophis, Drymarchon, Drymobius, Drymoluber, Erythrolamprus, Helicops, Imantodes, Lampropeltis, Leimadophis, Leptophis, Liophis, Lygophis, Ninia, Nothopsis, Oxybelis, Philodryas, Pliocercus, Pseudoboa, Pseustes, Rhadinaea, Rhinobothryum, Siphlophis, Spilotes, Stenorhina, Synophis, Tantilla, Thamnodynastes, Tretanorhinus, Tripanurgos, Xenodon
Dipsadinae
Dipsas, Sibon
Xenoderminae
Xenopholis
Hydrophiidae
Hydrophiinae
Pelamis
Viperidae
Crotalinae
Bothrops, Lachesis

ZOOGEOGRAPHY

It has been written many times about Ecuador that it, like ancient Gaul, "in tres partes divisa est." These three parts are the Pacific lowlands, the Andes, and the Amazonian slope. Actually, this is a broad generalization that tends to obscure more than it clarifies. It is true that each of the areas possesses a reptilian and amphibian faunule distinct from the others, but it is equally true that there are faunal units within each area almost as distinct one from the other. Thus, on the Pacific coast, there is a distinct and major faunal break which corresponds in general with the northern limit of the influence on the coast of the Humboldt Current. North of this line is a fauna in which Central American species and genera are strongly predominant, and, in fact, the Chocóan rain forest is to all intents and purposes an extension of the Caribbean rain forest of Panamá and Costa Rica. South of the limit of current influence there is a somewhat impoverished fauna, which has definite affinity with coastal Peru and perhaps northern Chile.

There are other such distinct units on the Pacific slope of the Andes. There is a distinct, "cliff-hanging" fauna, autochthonous between about 1000 and 3000 meters, quite distinct in species and even in a few genera from the lowlands of the Pacific. In addition, there appears to be an as yet inadequately explored

cloud forest on the west slope, investigation of which will almost certainly explain some of the difficulties currently encountered in working with the Pacific slope species.

In the interandean valleys the situation is similar. Although quite depauperate in snake species, what few there are in the region show that the fauna of the area is not uniform, but is zonally divided from north to south. There are many more species of snakes in the Loja hoya, for example, than in the Quito valley. Many of the taxa in the Loja region are invaders from the lowlands into an area that is, in part, at least, well watered and timbered, a situation not true in the north. Each valley is likely to show distinct changes in its reptilian and amphibian fauna from its neighbors, because of the alternation of drainage directions from east to west, and the correspondingly divergent faunas available for invasion. The only species that range from valley to valley are the hardy spirits such as *Atelopus* or some *Eleutherodactylus,* which I have found on the grassy plains well above treeline. These forms are able to transgress the horizontal steps of the ladder formed by the north-south parallels of the Andean chain in this country. The fauna of the northern part of the interandean area of Ecuador shows strong and distinct relationships with the Colombian highlanders, while the Peruvian fauna is predominant in the south, with genera such as *Telmatobius* and *Stenocercus* reaching their northern periphery there.

On the Amazonian slope, there are two and probably three different groups of snake species, differentiated not on their exclusive relationships in Ecuador, but on their more general distribution. All are found in Amazonian Ecuador, a comparatively miniscule region, and are, for the most part, sympatric. But one group is limited almost entirely to the Amazonian slope of the Andes in Colombia, Ecuador, and Peru, as well as immediately adjacent Brazil, while the second is composed of extremely wide-ranging forms which cover all of the Amazonian Basin to the Atlantic, reach in many cases to the Caribbean, and are found in some instances to northern Argentina and coastal southeastern Brazil. The third element, as yet poorly defined, appears to be similar to the first in its restriction to upper Amazonian areas, but is a more southerly group, ranging from Bolivia into Peru, and only reaching Ecuador on its southern borders. It is possible, in addition, that a cloud forest fauna may be found on the eastern slope, as well as on the western. It is an interesting anomaly of herpetological research in Ecuador that the entryway

to the Amazonian slope is through the Andes rather than over them, as it is on the Pacific slope. The valley of the Río Pastaza drops directly down from Ambato after the most modest of climbs, and plunges one directly into the upper reaches of the tropics, at Baños. As a consequence, one never sees the upper slopes of the eastern side under normal circumstances — certainly no one has ever worked them thoroughly.

This brief summary hardly does justice to the zoogeographic patterns in Ecuador, but the picture is much more enlightening when all reptiles and amphibians are included. I hope to prepare a more graphic and inclusive analysis when my knowledge of all groups is more complete.

OMISSIONS

It will be noted by anyone familiar with South American herpetology that some species long considered to include Ecuador in their range are omitted from this list. A case in point is *Crotalus durissus terrificus* Laurenti. The rattlesnake has long been considered Ecuadorian (Orcés V., 1942: 147), but I have been unable to locate any documented records for it. Klauber, in his recent review of the rattlesnakes (1956: 123) felt the same way, for he wrote, "General statements have been made to the effect that *C. d. terrificus* occurs in Eastern Ecuador, but no authentic records are available. Little is known concerning the presence of rattlesnakes in the western part of the Amazon Basin." I eliminated *Hypsiglena* from the fauna of Ecuador and of South America as a whole (Peters, 1956), and with it the unassignable name *Pseudodipsas fallax* K. Peters. *Tachymenis peruviana* Wiegmann has been recorded from the Pacific lowlands at Guayaquil (Amaral, 1925: 14), but Walker (1945: 14) examined the specimen, and assigned it to *Dryophylax nattereri*. I have seen the specimen, and agree with Walker, including it here in its current generic position under *Thamnodynastes*. *Dryadophis boddaerti heathi* Cope was indicated as Ecuadorian by Stuart (1941: 78), but no records are known, and the reason seems to be solely the availability in Ecuador of suitable habitat. *Drymarchon corais corais* Boie is certainly to be expected in Amazonian Ecuador, and previously has been included in that fauna, but I cannot document that inclusion with specimens.

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Key to the Genera of Snakes Known or Expected in Ecuador

*indicates a genus not yet known from Ecuador, but expected

1. Scales of uniform size around body, or ventrals only feebly enlarged . . 2
   Ventral scales distinctly larger than dorsals 9

2. Tail flattened laterally . . . . *Pelamis*
   Tail more or less rounded 3

3. Ventrals feebly enlarged; teeth in both jaws 4
   Ventrals not enlarged; teeth in upper or lower jaw, not both 5

4. Nostrils dorsal; body unicolor . . . . *Eunectes*
   Nostrils lateral; ringed pattern . . . . *Anilius*

5. Nasal bordering lip; 14 scale rows on body . . . . *Leptotyphlops*
   Nasal not bordering lip; more than 14 scale rows 6

6. Rostral and frontal not in contact 7
   Rostral in broad contact with frontal 8

7. Frontal pentagonal . . . . *Anomalepis*
   Frontal semicircular . . . . *Helminthophis**

8. Small, divided nasal; prefrontals present . . . . *Liotyphlops*
   Very large nasal (may be divided or not); no prefrontals . . . . *Typhlops*

9. Pit present between eye and nostril....10
No pit between eye and nostril....12

10. Tail with rattle on tip....*Crotalus**
Tail with horny tip, no rattle....11

11. Posterior subcaudals replaced by small scales; upper head scales granular, smooth or obtusely keeled....*Lachesis*
No small scales under tail; upper head scales imbricate or subimbricate....*Bothrops.*

12. Vestiges of pelvis and hind limbs present (not always visible externally); maximum body scale rows 30 or more....13
No vestiges of pelvis or hind limbs, externally or internally; maximum body scale rows 28 or less....16

13. Rostral reduced or absent, several small scales on vertical aspect of tip of snout....*Trachyboa*
Rostral large, extends from lip to dorsal surface of head....14

14. Dorsum and sides of head between eyes and tip of snout with many small, irregularly arranged scales....15
Dorsum and sides of head between eyes and tip of snout with large, regularly placed scales, often in pairs....*Epicrates*

15. Dark stripe from eye across temporal region; usually another dark stripe from tip of snout between eyes to mid-dorsum; no deep pits in labials....*Boa*
Temporal region unicolor, lacking dark stripe; no stripe from snout passing between eyes; if either stripe is present, deep pits in labials....*Corallus*

16. Top of head with small scales....*Nothopsis*
Top of head with large, regular plates....17

17. Tip of snout raised into a sharp point....*Phimophis**
Tip of snout rounded, not with hard, sharp point....18

18. Number of scale rows one head length anterior to anus equal to or only one less than number at midbody....19
Number of scale rows one head length anterior to anus at least two less than number at midbody....43

19. Scales in 19 or more rows....20
Scales in less than 19 rows at maximum....22

20. Prefrontals united into a single scale....*Synophis*
Prefrontals double....21

21. Ventrals less than 200....*Ninia*
Ventrals more than 200....*Clelia*

22. Anal single 23
Anal divided 35

23. Scale rows 17 24
Scale rows 15 or less 27

24. Prefrontals united into single scale, may show partial suture .... *Xenopholis*
Prefrontals not united 25

25. Subcaudals single .... *Pseudoboa*
Subcaudals divided 26

26. Ventrals less than 200 .... *Atractus*
Ventrals more than 200 .... *Clelia*

27. Vertebral scale row equal in size to other dorsals 28
Vertebral scale row larger than other dorsals 33

28. Internasals fused into single scale 29
Two internasal scales 30

29. Two prefrontal scales .... *Hydrops**
One prefrontal scale .... *Apostolepis**

30. Scale pits present .... *Drymoluber*
Scale pits absent 31

31. Poison fangs in upper jaw .... *Micrurus*
No poison fangs in upper jaw 32

32. No loreal; preocular present .... *Drepanoides* (which includes *Pseudoclelia*)
Loreal present; or, if absent, preocular absent .... *Atractus*

33. Labial beneath primary temporal greatly enlarged, and in contact with postocular, primary and secondary temporal .... *Sibon*
Labial beneath primary temporals not enlarged, no single labial in contact with postocular, primary and secondary temporals 34

34. Mental groove present .... *Imantodes*
Mental groove absent .... *Dipsas*

35. Scale rows 17 36
Scale rows 15 39

36. Internasals fused with anterior section of nasal .... *Stenorrhina*
Internasals distinct from nasal 37

37. Pattern of stripes, which may be so vague as to appear unicolor .... *Rhadinaea*
Pattern not of stripes, but never unicolor 38

38. Head sharply distinct from neck....*Imantodes*
Head and neck about same size....*Pliocercus*

39. Pattern of red, black, and yellow rings....40
Pattern not annulate....41

40. Loreal present....*Erythrolamprus*
Loreal absent....*Micrurus*

41. Mental widely separating first lower labials and in contact wtih anterior pair of chin shields....*Leptomicrurus*
Mental not in contact with anterior pair of chin shields; first lower labials in contact on midline....42

42. Internasals fused; nasals in contact....*Pseudoeryx**
Two internasals; nasal scales not in contact....*Tantilla*

43. Scales in even number of rows....44
Scales in odd number of rows....45

44. Scales at midbody in 10 or 12 rows....*Chironius*
Scales at midbody in 14, 16 or 18 rows....*Spilotes*

45. Some or all scale rows keeled....46
All scales smooth....61

46. Anal divided....47
Anal single....54

47. Maximum scale rows 19 or more....48
Maximum scale rows 17 or less....52

48. Scale pits present....49
Scale pits absent....51

49. Pattern of red and black rings....*Rhinobothryum*
Pattern not of red and black rings....50

50. Pupil round; dorsal scales oblique; green dorsum....*Philodryas*
Pupil elliptic; dorsal scales not oblique; grayish in color....*Thamnodynastes*

51. Usually three prefrontals; maxillary teeth subequal....*Tretanorhinus*
Two prefrontals; posterior maxillary teeth gradually increasing in size....*Helicops*

52. Scale rows 15....*Leptophis*
Scale rows 17....53

53. No loreal, prefrontal contacts labials; head elongate....*Oxybelis*
Loreal present, prefrontal does not contact labials; head not elongate 59

54. Prefrontals united into a single scale....55
Prefrontals paired, not fused into a single scale....56

55. A single keel on individual scales in the vertebral row....*Synophis*
Double keels on individual scales in the vertebral row....*Diaphorolepis*

56. Scales in 15 rows at maximum....57
Scales in 17 or more rows at maximum....58

57. Upper labials 6; lower labials 7....*Oxybelis*
Upper labials may be 7, usually 8 or more; lower labials 8 or more....*Leptophis*

58. Scale rows medially 17 or less....59
Scale rows medially more than 20....60

59. Subcaudals more than 110; maxillary teeth 32 or more, subequal *Dendrophidion*
Subcaudals less than 110; maxillary teeth 34 or less, posteriormost greatly increased in size....*Drymobius*

60. Less than 50 single subcaudals....*Tropidophis*
More than 100 double subcaudals....*Pseustes*

61. Anal single....62
Anal divided....77

62. No loreal; prefrontal in contact with labials....63
Loreal present; or, if absent, prefrontals do not contact labials....64

63. Two pairs of prefrontals, more than 21 scale rows at maximum *Tropidophis*
One pair of prefrontals, less than 21 scale rows at maximum....*Oxybelis*

64. Maximum scale rows 15 or less....*Dipsas*
Scale rows 17 or more....65

65. Maximum scale rows 17....66
Scale rows 19 or more....70

66. Body striped with light and dark brown, at least posteriorly *Thamnodynastes*
Body not striped....67

67. Body unicolor, no dark cross bands....*Drymarchon*
Body light with darker cross bands or spots....68

68. Head much larger than the very slim, vine-like body; eye very large....*Imantodes*
Head not or very slightly larger than body; eye not greatly enlarged....69

69. Ventrals less than 200....*Atractus*
Ventrals more than 200....*Clelia*

70. Anterior temporal single....71
Anterior temporals two or more....72

71. Scales in diagonal rows....*Xenodon*
Scales in regular, horizontal rows....*Oxyrhopus*

72. Dorsal pattern of complete yellow and red rings, separated by black rings....*Lampropeltis*
Dorsal pattern not of complete yellow and red rings....73

73. Labials excluded from eye by subocular row of scales....*Dugandia**
At least one labial enters orbit....74

74. Dorsum with dark bands, which are very narrow; interspaces 4-5 times as wide as blotches....*Tripanurgos*
Dorsum without bands, or, if bands are present, interspaces are not 4-5 times as wide as bands....75

75. Pattern of spots or numerous cross bands with very irregular zigzag borders; head shields variegated with light and dark; third to fifth anterior mandibular teeth very much enlarged....*Siphlophis**
Pattern not as above; anterior mandibular teeth may be enlarged with gradual decrease in tooth length toward posterior....76

76. Anterior mandibular teeth much the largest....*Oxyrhopus*
All mandibular teeth approximately the same size....*Clelia*

77. No loreal, prefrontal in contact with labials....*Oxybelis*
A loreal, or if absent, prefrontal not as described....78

78. Two or more anterior temporals....79
One anterior temporal....82

79. Posterior maxillary teeth grooved....*Thamnodynastes*
Posterior maxillary teeth without grooves....80

80. Posterior maxillary teeth enlarged, separated from other maxillary teeth by diastema....*Rhadinaea*
Posterior maxillary teeth not enlarged, no diastema....81

81. 19 scale rows....*Drymobius reissii* Peters 1868 [1]
17 or less scale rows....*Dryadophis*

82. Maximum scale rows 17 or less....83
Maximum scale rows 19 or more....88

83. Maximum scale rows 15....*Leptophis*
Maximum scale rows 17....84

84. Head short, much broader than slender neck; eye very large with vertical pupil....*Imantodes*
Head not or but slightly larger than neck; eye normal....85

[1] Described in Monatsb. Akad. Wiss. Berlin, 1868, p. 640 (Type Berlin Mus. 4507), from Guayaquil. I do not know to what genus it belongs, but it apparently does not fit in *Drymobius* as defined by Stuart (Occ. Pap. Mus. Zool. Univ. Mich., no. 236, 1932, p. 6). The type must be re-examined to assign the species to its proper genus.

85. Scale pits present....*Leimadophis*
Scale pits absent....86

86. No stripes on body....*Liophis*
Stripes present on body, often on posterior part only....87

87. Chin black with white spotting; dorsal dark brown color extends well onto tips of ventrals; rest of venter clear yellow with no spotting....*Rhadinaea*
Chin white with black spotting; dorsal ground color does not extend onto ventrals; all of venter spotted and blotched with black. *Lygophis*

88. Scale pits present....89
Scale pits absent....92

89. Scale pits double....90
Scale pits single....91

90. Vertical pupil; rounded ventrals; no clear line marking end of dorsal color on ventrals....*Leptodeira*
Round pupil; angulate ventrals; a clear light line on ventrals at edge of dorsal color....*Philodryas*

91. Body banded in young; bands may disappear in adults, which are then unicolor; scales disposed obliquely....*Xenodon*
Body striped at least posteriorly or some trace of spots or bars, at least anteriorly; scales in longitudinal rows on body....*Leimadophis*

92. Dorsum with bands....*Liophis*
Dorsum striped throughout length....93

93. First few dorsal scale rows very light, same color as venter, dark stripe above them; posteriormost maxillary teeth without grooves *Lygophis*
First few dorsal scale rows dark, darker than and contrasting with venter, light stripe above them; posteriormost maxillary teeth grooved *Coniophanes*

ANILIUS

Anilius scytale Linnaeus

Anguis scytale Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 228.—"Indiis" (RMS 3 cotypes).

Range: Guianas; Northern Brazil; Colombia; Ecuador; Peru. Amazonian drainage.

ANOMALEPIS

Anomalepis flavapices Peters

Anomalepis flavapices Peters, 1957, Amer. Mus. Novitates, no. 1851, p. 3.—Esmeraldas, Esmeraldas Province, Ecuador (JAP 2613).

Range: Lowlands of Northwestern Ecuador.

ATRACTUS

1. Loreal shield reduced to a minute scale or absent; prefrontals meeting supralabials ... *carrioni*
   Loreal shield well developed; prefrontals not meeting supralabials .. 2

2. Dorsal scales in 15 rows ... 3
   Dorsal scales in 17 rows ... 5

3. Loreal relatively short, about equal in length to length of postnasal; prefrontals broader than long, equal to or smaller than rostral; color pattern including red and black rings ... *elaps*
   Loreal long, between two and three times as long as postnasal; prefrontals longer than broad, much larger than rostral; no rings in color pattern ... 4

4. Maxillary teeth 10-11; supralabials 6 ... *roulei*
   Maxillary teeth 7-8; supralabials 8 (sometimes 7) ... *occipitoalbus*

5. Dorsal color pattern of bands, blotches or stripes ... 6
   Dorsal coloration uniformly dark brown or gray ... 12

6. Dorsal color pattern of longitudinal stripes ... 7
   Dorsal pattern of bands or blotches ... 11

7. Ventrals plus caudals less than 210 (range 164-196) ... 8
   Ventrals plus caudals 210 or more (range 222-240) ... *gaigeae*

8. No stripes along edges of ventrals; no dorsolateral blotches, although dorsolateral stripes present ... 9
   Stripes along edges of ventrals present, as are dorsolateral blotches .. 10

9. No vertebral stripe; maxillary teeth 8; hemipenes in males extending to level of 12th caudal ... *ecuadorensis*
   A vertebral stripe; maxillary teeth 6; hemipenes in males extending to level of 18th caudal ... *occidentalis*

10. A vertebral stripe present; ventrals plus caudals 164 ... *dunni*
    No vertebral stripe; ventrals plus caudals 194-196 ... *collaris*

11. Ventrals in males 148-172, in females 157-181, venter yellow spotted with dark ... *major*
    Ventrals in males 168-173, in females 177-184, venter unspotted yellow ... *multicinctus*

12. Venter pale brown with faint line along margins of ventrals *microrhynchus*
    Venter unicolor or with irregular dark brown markings medially ... 13

13. Ventrals in males more than 150, in females more than 160 ... 14
    Ventrals in males 142-144, in females 148-153 ... *lehmanni*

14. Loreal moderate, about 1½ times as long as postnasal....*modestus*
Loreal long, well over twice as long as postnasal.....15

15. Ventrals plus caudals 184-203; supralabials usually 8....*resplendens*
Ventrals plus caudals 215-223; supralabials usually 7....*paucidens*

Atractus carrioni Parker

Atractus carrioni Parker, 1930, Ann. Mag. Nat. Hist., ser. 10, vol. 5, p. 208.—Loja, Ecuador, 2200 m. (BM 1929.10.30.1, female).

Range: Intermontane valley of Loja, Ecuador.

Atractus collaris Peracca

Atractus collaris Peracca, 1897, Bol. Mus. Zool. Univ. Torino, vol. 12, p. 4.—Río Cononaco, Napo-Pastaza Province, Ecuador (TurM).

Range: Amazonian Ecuador and Peru.

Atractus dunni Savage

Rhabdosoma maculatum Bocourt, 1883, Miss. Sci. Mex., pt. 3, p. 539, pl. 34.—"Equateur." (PM 5986, female).

Atractus dunni Savage, 1955, Proc. Biol. Soc. Washington, vol. 68, p. 14.—Ecuador (substitute name for *Rhabdosoma maculatum* Bocourt, preoccupied).

Range: "Ecuador".

Atractus ecuadorensis Savage

Atractus ecuadorensis Savage, 1955, Proc. Biol. Soc. Washington, vol. 68, p. 15.—"Llangate Area," probably Llanganate Range, Tunguruhua Province, Ecuador (CNHM 23529, male).

Range: Known only from the type locality.

Atractus elaps Günther

Rhabdosoma elaps Günther, 1858, Cat. Coll. Snakes Brit. Mus., p. 241.—Guayaquil, Ecuador, probably in error (BM).

Range: The oriente of Ecuador, northern Peru, Bolivia, eastern Colombia, Venezuela, and western Brazil.

Atractus gaigeae Savage

Rhabdosoma maculatum Bocourt, 1883, (part), Miss. Sci. Mex., pt. 3, p. 540, pl. 35, fig. 1.

Atractus gaigeae Savage, 1955, Proc. Biol. Soc. Washington, vol. 68, p. 12.—Santiago-Zamora Province, Ecuador (UMMZ 82887, male).

Range: Amazonian lowlands of Ecuador.

Atractus lehmanni Boettger

Atractus lehmanni Boettger, 1898, Katal. Rept. Mus. Senckenberg, vol. 2, p. 80.—Cuenca, Azuay Province, Ecuador (Senck 8310a, 6 cotypes; MCZ 33513, cotype).

Range: Known only from the type locality.

Atractus major Boulenger

Atractus major Boulenger, 1894, Cat. Snakes Brit. Mus., vol. 2, p. 307.—Intac (BM 1946. 9.7.56); Pallatanga (BM 1946. 9.7.60); Canelos (BM 1946. 9.7.27, designated lectotype by Savage, Misc. Publ. UMMZ, No. 112, p. 50, 1960); and "W. Ecuador" (BM 1946. 9.7.57-59).

Range: Ecuador and Colombia on Amazonian slopes; Venezuela.

Atractus microrhynchus Cope

Atractus microrhynchus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 102.—Guayaquil, Ecuador (USNM 6693).

Range: Known only from type specimen.

Atractus modestus Boulenger

Atractus modestus Boulenger, 1894, Cat. Snakes Brit. Mus., vol. 2, p. 304, pl. 15, fig. 1.—"W. Ecuador" (BM 1946. 1.6.30, male).

Range: Western Ecuador.

Atractus multicinctus Jan

Rhabdosoma badium multicinctum Jan, 1865, *in* Jan and Sordelli, Icon. Ophidiens, vol. 10, pl. 4, fig. 5.—Lima, Peru, in error (Type unknown).

Range: Northwestern Ecuador into the Chocó of Colombia.

Atractus occidentalis Savage

Atractus occidentalis Savage, 1955, Proc. Biol. Soc. Washington, vol. 68, p. 16.—Mindo, Pichincha Province, Ecuador (BM 1916. 5.23.5).

Range: Higher Pacific slopes of the Andes in northwestern Ecuador.

Atractus occipitoalbus Jan

Rhabdosoma occipitoalbum Jan, 1862, Arch. per la Zool. Anat. Fisiol., vol. 2 (1), p. 16.—Andes, Ecuador, 4000 feet (MonM).

Rhabdosoma duboisi Boulenger, 1880, Bull. Soc. Zool. France, p. 44.—"Andes of Ecuador" (IRB, 2 cotypes).

Atractus orcesi Savage, 1955, Proc. Biol. Soc. Washington, vol. 68, p. 17.—Loreto, Napo-Pastaza Province, Ecuador (SU 15622).

Range: Eastern slopes of the Andes in Ecuador.

Atractus paucidens Despax

Atractus (*Atractopsis*) *paucidens* Despax, 1910, Bull. Mus. Hist. Nat. Paris, 1910, p. 372.—Santo Domingo de los Colorados, Ecuador (PM 06-245).

Range: Slopes of Andes in northwestern Ecuador.

Atractus resplendens Werner

Atractus torquatus resplendens Werner, 1901, Ver. Zool.-Bot. Ges. Wien,

vol. 51, p. 598.—Ecuador (Location of type unknown).
Range: Amazonian slopes of Ecuador.

Atractus roulei Despax

Atractus roulei Despax, 1910, Bull. Mus. Hist. Nat. Paris, p. 370.—Alausi, Ecuador, 2350 m. (PM 06-243).
Range: Southwestern Ecuador.

BOA

1. Scales in 81-95 rows; red areas on tail; body with 15-20 dark cross bars; black median line on head without lateral processes between eyes . . . . *constrictor constrictor*
   Scales in 61-79 rows; no red areas on tail; body with 22-30 dark cross bars; black median line on head with lateral processes between eyes . . . . *constrictor imperator*

Boa constrictor constrictor Linnaeus

Boa constrictor Linnaeus, 1758, Syst. Nat., 10th Ed., vol. 1, p. 215.—"Indiis" (RMS, 2 cotypes).
Range: Amazonian South America to Argentina and Paraguay; Trinidad; Tobago.

Boa constrictor imperator Daudin

Boa imperator Daudin, 1803, Hist. Nat. des Rept., vol. 5, p. 150.—"Mexico," restricted to Córdoba, Veracruz, Mexico, by Smith and Taylor, U. Kans. Sci. Bull., vol. 33 (8), p. 347, 1950; E. R. Dunn indicated in correspondence that he believed the type came from the Colombian Chocó (Type no longer in PM, probably destroyed).
Range: Mexico south to northwestern South America west of the Andes to Ecuador and Peru.

BOTHROPS

1. Non-prehensile tail 2
   Prehensile tail 9

2. Subcaudals all or greater part in two rows 3
   Subcaudals all or greater part single 7

3. Scales on the vertex and occiput more or less strongly keeled; dorsal scales strongly keeled 4
   Upper head scales smooth; dorsal scales not strongly keeled . . . *xanthogramma*

4. Second upper labial forming anterior border of loreal pit 5
   Loreal pit separated from labials . . . . *m. micropthalma*

5. Scales in 25-29 rows . . . . *a. atrox*
   Scales in 21-23 rows 6

6. Keels on dorsal scales much shorter than scale itself; ventrals 156-174; subcaudals 47-64 . . . *pulchra*
Keels on dorsal scales reach extremity of scale; ventrals 144-155; subcaudals 38-44 . . . . *lojana*

7. Second upper labial forming anterior border of loreal pit . . . . *castelnaudi*
Loreal pit separated from the labials 8

8. Double internasals; ventrals 125-131; subcaudals 44-50 . . . . *hyoprora*
Single internasal; ventrals 130-145; subcaudals 24-35 . . . . *nasuta*

9. Subcaudals all or greater part in two rows 10
Subcaudals all or greater part single 12

10. Dorsal scale rows in 19-21 rows 11
Dorsal scale rows in 25-35 rows 13

11. Scales in 19 rows . . . . *alticola*
Scales in 21 rows . . . . *albocarinata*

12. Keels on dorsal, dorsal head, and dorsal caudal scales all whitish, giving a finely striated appearance . . . . *albocarinata*
Keels on dorsal scales same color as scale itself . . . . *schlegeli*

13. Green, uniform or speckled with black; a yellow lateral streak or series of spots on first row of dorsal scales . . . . *bilineata*
Pallid greenish-gray, with rounded, yellow-bordered black spots *punctata*

Bothrops albocarinata Shreve

Bothrops albocarinata Shreve, 1934, Occ. Pap. Boston Soc. Nat. Hist., vol. 8, p. 130.—Pastaza River between Canelos and Marañon River, Ecuador (MCZ 36989).

Range: Known only from the Pastaza River drainage in Ecuador.

Bothrops alticola Parker

Bothrops alticola Parker, 1934, Ann. Mag. Nat. Hist., ser. 10, vol. 14, p. 272.—5 km. east of Loja, Ecuador, 9200 feet (BM 1933. 6.24.115, male).

Range: Known only from the vicinity of the type locality.

Bothrops atrox atrox Linnaeus

Coluber atrox Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 222.—"Asia," Restricted to Surinam by Schmidt and Walker, Zool. Ser. Field Mus. Nat. Hist., vol. 24, p. 295, 1943 (Type unknown).

Range: Amazonian Brazil and northern Bolivia north to Mexico. Occurs on Pacific and Amazonian slopes in Ecuador.

Bothrops bilineata Wied

Cophias bilineata Wied, 1825, Beitr. Naturgesch. Brasil, vol. 1, p. 483.—No type locality given (Type unknown).

Range: Bolivia; Peru; Ecuador; Brazil; in their Amazonian parts.

Bothrops castelnaudi Duméril, Bibron and Duméril

Bothrops castelnaudi Duméril, Bibron and Duméril, 1854, Erp. Gen., vol. 7 (2), p. 1511.—South America (PM 1582).

Bothrops quadriscutatus Peters, 1861, Monatsb. Akad. Wiss. Berlin, p. 358.—Quito, Ecuador (BerM).

Range: Northern Brazil; Colombia; Ecuador; and eastern Peru.

Bothrops hyoprora Amaral

Bothrops hyoprora Amaral, 1935, Mem. Inst. Butantan, vol. 9, p. 222.—La Pedrera, Colombia (IB 9199, male).

Range: Southern Colombia; eastern Ecuador; Peru; and the state of Amazonas in Brazil.

Bothrops lojana Parker

Bothrops lojana Parker, 1930, Ann. Mag. Nat. Hist., ser. 10, vol. 5, p. 568.—Loja City, Ecuador, 2200 m. (BM 1930. 1.30.1).

Range: Vicinity of type locality.

Bothrops micropthalma micropthalma Cope

Bothrops micropthalmus Cope, 1876, Jour. Acad. Nat. Sci. Philadelphia, vol. 8 (2), p. 182.—From between Balsas Puerto and Moyabamba, Peru (ANSP 11515).

Lachesis pleuroxanthus Boulenger, 1912, Ann. Mag. Nat. Hist., ser. 8, vol. 10, p. 423.—Alpayaca, Ecuador (BM 1946. 1.19.89).

Range: Amazonian Peru and Ecuador.

Bothrops nasuta Bocourt

Bothrops nasutus Bocourt, 1868, Ann. Sci. Nat., ser. 5, vol. 10, p. 202.—Unknown.

Range: Pacific slope of Ecuador and Colombia; east coast of Central America to Mexico.

Bothrops pulchra Peters

Trigonocephalus pulcher Peters, 1862, Monatsb. Akad. Wiss. Berlin, p. 672.—Quito, Ecuador (BerM 3868, 3 syntypes).

Range: Peru and Ecuador in the Amazonian lowlands.

Bothrops punctata Garcia

Lachesis punctata Garcia, 1896, Ofid. Venen. del Cauca, Cali, Colombia,

p. 31, pl. 8.—"Las montañas del Dagua," Colombia—according to E. R. Dunn, this is on the Pacific Coast (Type non-existent).
Lachesis monticellii Peracca, 1910, Annu. Mus. Napoli, vol. 3 (12), p. 2.—"America tropicale?" (UNZM).
Range: Panamá; Colombia; Ecuador; in the Chocó region.

Bothrops schlegelii schlegelii Berthold

Trigonocephalus schlegelii Berthold, 1846, Abh. Ges. Wiss. Gottingen, vol. 3, p. 13, tab. b, figs. 5-6.—"New Grenada, Provinz Popayan," which Dunn and Stuart, Copeia, 1951, p. 56, say is same as Popayan, Colombia (GottM).
Lachesis nitidus Günther, 1859, Proc. Zool. Soc. London, p. 414.—"Western Andes of Ecuador" (BM 60.6.16.83).
Range: Chocó Region of Panamá, Colombia, and Ecuador.

Bothrops xanthogramma Cope

Trigonocephalus xanthogrammus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 110.—Pallatanga, Ecuador (ANSP 9978).
Range: Apparently to be found in the highlands of Ecuador and Colombia.

CHIRONIUS

1. Scale rows 10 on anterior part of body 2
   Scale rows 12 on anterior part of body 3

2. All dorsal scale rows keeled to level of anus except paravertebrals and lowermost row .... *grandisquamis*
   Only vertebral rows (one on each side of body) with keels, other dorsal rows smooth .. *schlüteri*

3. Dark brown or blackish above, vertebral line pale brown, ventral and subcaudal scales yellow with a fine black edge .... *carinatus*
   Keeled scales with large spots at their base, which gives the appearance of a yellow vertebral line; lateral scales with diagonal yellow streaks .... *flavopictus*

Chironius carinatus Linnaeus

Coluber carinatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 223.—"Indiis" (RMS).
Range: Central America; Tropical South America; Trinidad; Guadelupe; San Vicente.

Chironius flavopictus Werner

Herpetodryas carinatus flavopicta Werner, 1909, Mitt. Naturh. Mus. Hamburg, vol. 26, p. 220.—Guayaquil, Ecuador (HM-V118, 2 cotypes).
Range: Known from the type locality and the headwaters of the Río Congo.

Chironius grandisquamis Peters

Spilotes grandisquamis Peters, 1868, Monatsb. Akad. Wiss. Berlin, p. 451.—Costa Rica (BerM).

Range: Costa Rica; Panamá (MVZ 35559); northwestern Ecuador.

Chironius schlüteri Werner

Herpetodryas schlüteri Werner, 1899, Zool. Anz., vol. 22, p. 115.—Napo, Ecuador (VM).

Range: Amazonian slopes of Ecuador.

CLELIA

1. 19 scale rows . . . . *clelia clelia*
   17 scale rows . . . . *clelia scytalina*

Clelia clelia clelia Daudin

Coluber clelia Daudin, 1803, Hist. Nat. Rept., vol. 6, p. 330, pl. 78.—"Surinam" (Type no longer in PM, probably destroyed).

Range: Central America to Argentina and Uruguay.

Clelia clelia scytalina Cope

Scolecophis scytalina Cope, 1866, Proc. Acad. Nat. Sci. Philadelphia, vol. 18, p. 320, (publ. 1867).—San Juan Bautista, Tabasco, Mexico (USNM 6581).

Barbourina equatoriana Amaral, 1924, Jour. Washington Acad. Sci., vol. 14 (9), p. 201.—Guayaquil, Ecuador (USNM 62790).

Range: Apparently very disjunct: Parts of Mexico; interior highlands of Colombia (Dunn, Caldasia, vol. 3 (12), p. 201, 1944); western Ecuador.

CONIOPHANES [2]

1. Dorsals in 19 rows; 3-5 black lines on top of head between eyes *dromiciformis*
   Dorsals in 21 rows, no black lines between eyes . . . . *f. fissidens*

Coniophanes dromiciformis Peters

Tachymenis dromiciformis Peters, 1863, Monatsb. Akad. Wiss. Berlin, p. 273.—Guayaquil, Ecuador (BerM 3729-2 syntypes, 3730-3 syntypes, and 4550-3 syntypes).

Coniophanes signatus Garman, 1892, Bull. Essex Inst., vol. 24, p. 91.—Guayaquil, Ecuador (CNHM 16941).

Range: Ecuador and Peru, on the Pacific coastal areas.

[2] *Coniophanes brevifrons* Bailey, 1937, described from "Ecuador," is actually a species known from San Andres Island, according to Dunn and Saxe, Proc. Acad. Nat. Sci. Phila., vol. 102, p. 162, 1950.

Coniophanes fissidens fissidens Günther

Coronella fissidens Günther, 1858, Cat. Snakes Brit. Mus., p. 36.—"Mexico," restricted to San Andres Tuxtla, Vera Cruz, by Smith and Taylor, 1950 (6 cotypes, BM 56.3.17.35-36, 57.7.31.48, 57.7.31.54, 60.6.17.17, and one unnumbered specimen).

Range: Central Vera Cruz south on Atlantic Coast of Central America to northwestern Ecuador, avoiding high mountains and the Yucatan Peninsula.

CORALLUS

1. Nasals not in contact; subcaudals less than 85 2
   Nasals in contact; subcaudals more than 100 . . . . *e. enydris*

2. Dorsum green (dark blue in preservative) with white line down spine, lateral branches down sides; which may break into row of spots . . . . *caninus*
   Dorsum light, with large, pale-reddish blotches, margined by darker color 3

3. Two medium-sized lateral internasals, separated by two medial internasals, arranged one behind the other; four supraloreals . . *annulatus blombergi*
   Large pair of lateral internasals, which are in contact anteriorly but separated posteriorly by a single medial internasal; three supraloreals . . . . *annulatus colombianus*

Corallus annulatus blombergi Rendahl and Vestergren

Boa annulata blombergi Rendahl and Vestergren, 1941, Ark. für Zool., vol. 33A (5), p. 1, figs. 6-7.—Río Zamora, E. Ecuador (RMS 3141).

Range: Known only from the type locality.

Corallus annulatus colombianus Rendahl and Vestergren

Boa annulata colombiana Rendahl and Vestergren, 1940, Ark. für Zool., vol. 33A (1), p. 2.—Cabeceras, Chocó, Colombia (RMS).

Range: Chocó of Colombia and Ecuador.

Corallus caninus Linnaeus

Boa canina Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 215.—"America." (Type unknown).

Range: Colombia; Venezuela; Guianas; Brazil; Bolivia; Ecuador.

Corallus enydris enydris Linnaeus

Boa enydris Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 215.—"America" (RMS 1 specimen).

Range: N. Brazil; Bolivia; Ecuador; Peru; Guianas.

DENDROPHIDION

1. Subcaudals less than 175 2
   Subcaudals more than 175 .... *dendrophis*

2. Dorsum striped; a black streak through eye .... *bivittatum*
   Dorsum unicolor; no black streak through eye .... *brunneum*

Dendrophidion bivittatum Duméril, Bibron and Duméril

Leptophis bivittatus Duméril, Bibron and Duméril, 1854, Erp. Gen., vol. 7 (1), p. 540.—"New Grenada" (PM 517 and PM 6.3460, 2 cotypes).

Range: Ecuador; Colombia; and Panamá. A Chocóan distribution.

Dendrophidion brunneum Günther

Herpetodryas brunneus Günther, 1858, Cat. Snakes Brit. Mus., p. 116.—"Guayaquil" (BM 1946.1.12.98).

Range: Interandean valleys of Ecuador.

Dendrophidion dendrophis Schlegel

Herpetodryas dendrophis Schlegel, 1837, Physiog. Serpents, vol. 2, p. 196.—"Cayenne" (Types not in PM, probably non-existent).

Range: Amazonian region of Ecuador and Guianas.

DIAPHOROLEPIS

Diaphorolepis wagneri Jan

Diaphorolepis wagneri Jan, 1863, Elenco Sist., p. 94.—Andes of Ecuador (MonM).

Synophis bicolor Peracca, 1896, Bol. Mus. Zool. Anat. Comp. Torino, no. 266, p. 1.—"Central America" (TurM).

Range: Western Ecuador in the lowlands, presumably into Central America.

DIPSAS

1. Dorsal pattern of broad, dark brown or black bands that are much wider than interspaces and have vertical edges, interspaces pink or red in life (*articulata* group) 2
   Pattern not as above 3

2. At least one pair of labials in contact behind mental .... *gracilis*
   Mental in contact with paired chin shields .... *temporalis*

3. Dorsal pattern of rounded, dark brown or black blotches or saddles on sides, interspaces tawny brown (*catesbyi* group) 4
   Dorsal pattern not as above 6

4. Two prefrontals; dorsum of head unicolor 5
   Prefrontals usually fused; dorsum of head variegated and streaked with white .... *vermiculata*

5. Blotches narrower at vertebral row than laterally; loreal does not enter eye .... *catesbyi*
   Blotches saddle-shaped, wider at vertebral row than laterally; loreal enters eye .... *pavonina*

6. Dorsal blotches triangular or lozenge-shaped in appearance, usually widest at ventrals, with yellow spot between corners of blotches at ventrals (*indica* group) 7
   Dorsal pattern not as above 8

7. Occipital region not streaked, may be spotted; first dorsal blotch broadly fused along middorsal line .... *indica indica*
   Occipital region longitudinally streaked; first dorsal blotch pair separated by light line at vertebrals .... *indica ecuadorensis*

8. Dorsal ground color of light browns and tans, with narrow blotches that are higher than wide, and much narrower than interspaces (at least posteriorly), latter streaked, spotted or stippled throughout (*variegata* group) 9
   Dorsal pattern not as above 10

9. Dark brown spots on head unite on frontals to form U-shaped mark, posterior tips of "U" often fused to first dorsal blotch .... *variegata nicholsi*
   Dark brown spots on head not fused on frontal, do not extend to first dorsal blotch .... *variegata variegata*

10. Dorsal blotches wider than interspaces, little contrast between them; centers of blotches often considerably lightened, so that blotch resembles paired ellipses (*ellipsifera* group) 11
    Dorsal pattern not as above (*pratti* group) 12

11. Centers of dorsal blotches very light, so that blotch resembles paired ellipses, on all individuals; chin heavily spotted; venter with two parallel dark streaks; ventrals often less than 170, subcaudals less than 80 .... *ellipsifera*
    Centers of dorsal blotches lightened only in adults, not in juveniles, and never so light that the blotch resembles paired ellipses; chin not or sparsely spotted; venter with large rectangular blotches between ends of neighboring dorsal blotches; ventrals more than 175; subcaudals more than 79 .... *oreas*

12. Dorsal ground color yellowish-brown; first few dorsal blotches fused ventrally; usually two pairs of lower labials in contact behind mental .... *latifasciata*
    Dorsal ground color reddish-brown, or, in old adults, interspaces same color as blotches; usually all dorsal blotches fail to meet on venter; usually less than two pairs in contact behind mental .... *latifrontalis*

Dipsas catesbyi Sentzen

Coluber catesbeji Sentzen, 1796, Meyer's Zool., Arch. 2, p. 66.—Unknown.

Range: Amazonian Basin, from the Andean slopes of Bolivia, Peru, Ecuador, and Colombia to coast of Venezuela and British Guiana, and through northern half of Brazil.

Dipsas ellipsifera Boulenger

Leptognathus ellipsifera Boulenger, 1898, Proc. Zool. Soc. London, p. 117, pl. 12, fig. 2.—Ibarra, Ecuador (BM 1946.1.21.26-29).

Range: Western slopes of Ecuadorian Andes.

Dipsas gracilis Boulenger

Leptognathus gracilis Boulenger, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 9, p. 57.—St. Javier, Ecuador (BM 1946.1.21.24-25, 2 males).

Leptognathus hammondi Boulenger, 1920, Ann. Mag. Nat. Hist., ser. 9, vol. 6, p. 110.—Guatea (=Gualea?), Ecuador (BM 1946.1.20.95, female).

Sibynomorphus macrostomus Amaral, 1924, Jour. Washington Acad. Sci., vol. 14, p. 9.—Ecuador (USNM 14047).

Range: Humid forests of coastal northwestern Ecuador.

Dipsas indica indica Laurenti

Dipsas indica Laurenti, 1768, Syn. Rept., p. 90.—"Ceylon," restricted to Amazonian region of South America by Peters, Misc. Publ. Univ. Mich. Mus. Zool. no. 114, p. 68, 1960. (Original type unknown, iconotype designated as pl. 43, fig. 5, of Seba, 1734, Peters, *loc. cit.*, p. 68).

Range: Amazonian basin, in Brazil, Colombia, British Guiana, Ecuador, and Peru.

Dipsas indica ecuadorensis Peters

Dipsas indica ecuadorensis Peters, 1960, Misc. Publ. Mus. Zool. Univ. Mich., no. 114, p. 81.—Río Solis, Caveceras del Río Bobonaza, 14 km. ESE of Puyo, Napo-Pastaza Province, Ecuador (UMMZ 118064, male).

Range: Known only from the Amazonian drainage of Ecuador.

Dipsas latifasciata Boulenger

Leptognathus latifasciata Boulenger, 1913, Ann. Mag. Nat. Hist., ser. 8, vol. 12, p. 72.—Upper Marañon River, eastern Peru (BM 1946.1.20.77).

Range: Amazonian slopes of northern Peru and extreme southern Ecuador.

Dipsas latifrontalis Boulenger

Leptognathus latifrontalis Boulenger, 1905, Ann. Mag. Nat. Hist., ser.

7, vol. 15, p. 561.—Aricaqua, Venezuela, 1000 meters (BM 1946.1.20.98, female).

Leptognathus palmeri Boulenger, 1912, Ann. Mag. Nat. Hist., ser. 8, vol. 10, p. 422.—El Topo, Río Pastaza, Ecuador (BM 1946.1.20.86, male).

Range: Lower Amazonian slopes from Venezuela to southern Ecuador.

Dipsas oreas Cope

Leptognathus oreas Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 109.—Elevated valley of Quito, Ecuador, probably in error (ANSP 10115, male).

Leptognathus andiana Boulenger, 1896, Cat. Snakes Brit. Mus., vol. 3, p. 452, pl. 23, fig. 2.—Quito, Ecuador, probably in error (BM 1946.1.20.12).

Range: Higher parts of the western slope of the Andes in Ecuador.

Dipsas pavonina Schlegel

Dipsas pavonina Schlegel, 1837, Physion. Serp., vol. 2, p. 280.—"Guyanes" (PM, cotype not locatable, and MPB, 4 cotypes).

Range: Guianas to Para, Brazil and to Amazonian slopes of the Andes; Colombia to Bolivia.

Dipsas temporalis Werner

Leptognathus temporalis Werner, 1909, Mitt. Naturh. Mus. Hamburg, vol. 26, p. 241.—Esmeraldas, Ecuador (formerly HM, now destroyed).

Range: Chocó area of northwestern Ecuador, Colombia, and Atlantic coast of Panamá.

Dipsas variegata variegata Duméril, Bibron, and Duméril

Leptognathus variegatus Duméril, Bibron, and Duméril, 1854, Erp. Gen., vol. 7, p. 477.—"Surinam" (PM 7299, and LeyM, one cotype).

Leptognathus robusta Müller, 1923, Zool. Anz., vol. 57, p. 155.—East Ecuador (ZSBS 622/1920).

Range: Venezuela, Guianas, Ecuador, and Peru.

Dipsas variegata nicholsi Dunn

Sibynomorphus nicholsi Dunn, 1933, Copeia, p. 193.—Mid-basin of Chagres River and mouth of Pequeni River, Panama (MCZ 37884, head only, sex unknown).

Range: Atlantic slope of Panamá to northwestern Ecuador.

Dipsas vermiculata Peters

Dispsas vermiculata Peters, 1960, Misc. Publ. Mus. Zool. Univ. Mich., no. 114, p. 65.—Chichirota, Lower Bobonaza River, Napo-Pastaza Province, Ecuador (UMMZ 118063, male).

Range: Amazonian slopes at lower elevations in Ecuador and Peru.

DREPANOIDES

Drepanoides anomalus Jan

Clelia anomala Jan, 1863, Elenco Sist., p. 92.—"Brasile" (type in Neuchatel).

Pseudoclelia guttata Rendahl and Vestergren, 1941, Ark. für Zool., vol. 33A (5), p. 10.—Río Pastaza between Río Puyo and Río Copataza, Ecuador (RMS 3172).

Range: Amazonian slopes of Peru and Ecuador.

DRYADOPHIS [3]

1. Supralabials usually 8; body pattern of alternating dorsal and lateral dark blotches . . . . *pulchriceps*
   Supralabials normally 9; body pattern striped, unicolor or narrowly banded 2

2. Single light lateral stripe on scale rows 4, 5, and 6 . . . . *heathi**
   Either no dorsal striping or a single light lateral stripe involving only rows 4, 5 . . . . *boddaerti*

Dryadophis boddaerti boddaerti Sentzen

Coluber boddaerti Sentzen, 1796, Ophiol. Frag., Meyer's Zool. Arch., vol. 2, p. 59.—Type and type locality unknown.

Coluber fasciatus Rosen, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 172, pl. 11, fig. 2.—Balao, Ecuador (LunM).

Herpetodryas reticulata Peters, 1863, Monatsb. Akad. Wiss. Berlin, p. 285.—Region of Guayaquil, Ecuador (BerM 4504).

Range: Humid areas of northern South America to the limits of the Amazon Basin.

Dryadophis pulchriceps Cope

Masticophis pulchriceps Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, vol. 2, p. 105.—Plateau Valley of Quito, Ecuador (ANSP 5710, formerly USNM 6704).

Range: Guaymas Basin and more humid habitats of West Central Ecuador.

DRYMARCHON

1. Belly and tail light throughout their length, no *distinctive* dark marks

[3] The range for *Dryadophis boddaerti heathi* Cope is given by Stuart, Misc. Publ. Univ. Mich. Mus. Zool. no. 49, p. 78, 1941, as "arid coastal desert from Ecuador possibly as far south as Chile," but no specimens are known from Ecuador, and the range as given is based upon the distribution of apparently suitable habitat.

on edges of subocular labials; in adults, anterior portion of body darker than posterior part and tail . . . . *c. corais*"
Posterior part of body and all of tail black above and below, light brown anteriorly, black marks on subocular labials sharply defined *corais melanurus*

Drymarchon corais melanurus Duméril, Bibron and Duméril

Spilotes melanurus Duméril, Bibron and Duméril, 1854, Erp. Gen., vol. 7 (1), p. 224.—"Mexico" (PM 638; 3185; 3354; 3 cotypes).
Drymarchon corais melanocercus Smith, 1941, Jour. Washington Acad. Sci., vol. 31, p. 473.—(A substitute name for *D. c. melanurus*, a secondary homonym).
Range: Pacific slopes of Colombia and Ecuador; Central America to Veracruz on the Atlantic slope and to Nicaragua on the Pacific slope.

DRYMOBIUS

Drymobius rhombifer Günther

Coryphodon rhombifer Günther, 1860, Proc. Zool. Soc. London, p. 236.—Esmeraldas, Ecuador (BM 1946.1.12.94).
Range: Panamá; Nicaragua; Costa Rica; Colombia; Ecuador; Peru.

DRYMOLUBER

Drymoluber dichrous Peters

Herpetodryas dichroa Peters, 1863, Monatsb. Akad. Wiss. Berlin, p. 284.—Brazil; Surinam (BerM 1661-62, 2 syntypes).
Herpetodryas occipitalis Günther, 1868, Ann. Mag. Nat. Hist., ser. 4, vol. 1, p. 430.—Pebas, "Ecuador" (BM 1946.1.14.61).
Spilotes piceus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 105.—Napo or Upper Marañon, Ecuador (Formerly USNM 6660, now lost).
Range: Colombia; Ecuador; eastern Peru; northern Brazil.

EPICRATES

Epicrates cenchria cenchria Linnaeus

Boa cenchria Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 215.—"Surinami" (RMS).
Range: Amazonian Basin and coastal Guianas.

ERYTHROLAMPRUS

1. Black annuli arranged in diads . . . . *aesculapii aesculapii*
Black annuli not arranged in diads, regularly distributed 2

2. Dorsal blotches and interspaces approximately equal in width.... *guentheri*
   Dorsal blotches much narrower than interspaces 3

3. Black collar covering posterior tips of parietals and several scales on midline of neck.... *mimus micrurus*
   Black collar absent; represented by spots; or only about one scale row wide on midline, diverging to about three scales on sides of neck.... *mimus mimus*

Erythrolamprus aesculapii aesculapii Linnaeus

Coluber aesculapii Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 220.—"Indiis." (RMS).

Range: Amazonian South America.

Erythrolamprus guentheri Garman

Erythrolamprus guentheri Garman, 1883, Mem. Mus. Comp. Zool. Harvard, vol. 8 (3), p. 154.—"Mexico (?)." (BM 1946.1.8.5-6, 1946.1.8. 38).

Range: Amazonian slopes of Ecuador.

Erythrolamprus mimus mimus Cope

Opheomorphus mimus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 307.—"High regions of Ecuador or New Grenada." (ANSP 3689).

Range: Eastern Peru and Ecuador.

Erythrolamprus mimus micrurus Dunn and Bailey

Erythrolamprus mimus micrurus Dunn and Bailey, 1939, Bull. Mus. Comp. Zool. Harvard, vol. 86 (1), p. 12.—Mine at Santa Cruz de Cana in Darien, Panamá, 2000 ft. (MCZ 31828, female).

Range: Chocó of Panamá, Colombia, and northwestern Ecuador.

EUNECTES

Eunectes murinus Linnaeus

Boa murina Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 215.—"America" (GothM).

Range: Amazonian South America.

HELICOPS

1. Scales in 19 rows; dorsum with more or less regular dark brown, black-edged cross bars.... *angulata*

2. Scales in 23-25 rows; dorsum with four series of confluent spots, upper two rows may merge anteriorly.... *pastazae*

Helicops angulata Linnaeus

Coluber angulatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 21.—"Asia" (RMS).

Range: Colombia; Venezuela; Guianas; Northern Brazil; Bolivia; Peru; Ecuador.

Helicops pastazae Shreve

Helicops pastazae Shreve, 1934, Occ. Pap. Boston Soc. Nat. Hist., vol. 8, p. 129.—Pastaza River, from Canelos to Marañon River, Ecuador (MCZ 36993).

Range: Amazonian Ecuador.

IMANTODES

1. Scale rows 17 2
   Scale rows 15 .... *lentiferus*

2. Vertebral scales not twice as wide as other dorsals; frontal twice as long as wide; dorsum with small, indistinct spots .... *inornatus*
   Vertebral scales more than twice as wide as other dorsals; frontal not twice as long as wide; dorsum with large brown saddles .... *cenchoa cenchoa*

Imantodes cenchoa cenchoa Linnaeus

Coluber cenchoa Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 226.—America (type unknown).

Range: South America including Paraguay, Bolivia and Argentina; Trinidad.

Imantodes inornatus Boulenger

Himantodes inornatus Boulenger, 1896, Cat. Snakes Brit. Mus., vol. 3, p. 88, pl. 5, fig. 1.—Hacienda Rosa de Jerico, Nicaragua (BM 1946.1.2.63).

Range: Nicaragua, Costa Rica, Panamá, and NW Ecuador (presumably also Chocó Coast of Colombia).

Imantodes lentiferus Cope

Himantodes lentiferus Cope, 1894, Amer. Nat., vol. 28, p. 613.—Pebas "Ecuador" (Peru), and "E. Ecuador" (2 cotypes, one ANSP 11459, other unknown).

Range: Amazonas, Brazil; and Amazonian Ecuador.

LACHESIS

Lachesis muta muta Linnaeus

Crotalus mutus Linnaeus, 1766, Syst. Nat., 12th ed., vol. 1, p. 373.—"Surinami" (Type unknown).

Range: Panamá; Venezuela; Colombia; Guianas; Ecuador; Peru; Brazil; Bolivia; Trinidad. Found in the lowlands on both the Pacific and Amazonian slopes in Ecuador.

LAMPROPELTIS

Lampropeltis doliata micropholis Cope

Lampropeltis micropholis Cope, 1861, Proc. Acad. Nat. Sci. Philadelphia, 1860 (1861), p. 257.—Panama (ANSP 3427).

Range: Panamá; Chocó of Colombia and Ecuador.

LEIMADOPHIS

1. Maximum scale rows on body 17 2
   Maximum scale rows on body 19 7

2. Subcaudals more than 46 3
   Subcaudals less than 46 .... *pygmaeus*

3. No black nape spots dorsally 4
   A pair of black nape spots dorsally .... *bimaculatus lamonae*

4. Two preoculars .... *epinephalus ecuadorensis*
   One preocular 5

5. Belly unspotted, unicolor yellowish white .... *albiventris*
   Belly blotched 6

6. Ventrals less than 150 .... *reginae*
   Ventrals more than 155 .... *fraseri*

7. Belly yellow with dark spotting 8
   Belly immaculate .... *typhlus*

8. Dark streak on side of head, passing through eye 9
   No dark streak passing through eye .... *poecilogyrus*

9. Two preoculars; venter of tail yellow with square black blotches, may be entirely black .... *taeniurus*
   One preocular; venter of tail yellowish, speckled with olive .... *simonsi*

Leimadophis albiventris Jan

Liophis reginae albiventris Jan, 1863, Arch. per la Zool., vol. 2 (2), p. 83.—"Western Andes" (MonM) and "Fra Lacatunga e Guayaquil" (Type no longer in PM).

Ophiomorphus alticolus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 102.—Valley of Quito, Ecuador (Formerly USNM 6703, now lost).

Range: Found in the lowlands on both sides of the Andes in Ecuador. Its range elsewhere in South America is obscured at present by erroneous use of the name in the literature.

Leimadophis bimaculatus lamonae Dunn

Leimadophis bimaculatus lamonae Dunn, 1944, Caldasia, vol. 10, p. 486. —Sonson, Antioquia, Colombia, 2410 m. (IdlS).

Range: Known from the type locality and "Equateur" (Laurent, Bull. Inst. Roy. Sci. nat. Belg., vol. 25 (9), p. 8, 1949).

Leimadophis epinephalus ecuadorensis Laurent

Leimadophis epinephalus ecuadorensis Laurent, 1949, Bull. Inst. Roy. Sci. nat. Belg., vol. 25 (9), p. 8.—"Equateur" (IRB 5028—I.G. no. 3267).

Range: Known only from the type locality.

Leimadophis fraseri Boulenger

Liophis fraseri Boulenger, 1894, Cat. Snakes Brit. Mus., vol. 2, p. 131, pl. 6, fig. 2.—"W. Ecuador" (BM 1946.1.6.63, female).

Range: Western Ecuador.

Leimadophis poecilogyrus Wied

Liophis poecilogyrus Wied, 1825, Beitr. Naturgesch. Brazil, vol. 1. p. 371.—Unknown.

Range: Argentina and Uruguay north to Amazonian Brazil and Ecuador.

Leimadophis pygmaeus Cope

Liophis pygmaeus Cope, 1868, Proc. Acad. Nat. Sci., Philadelphia, p. 103.—From Napo or neighboring part of Marañon, Ecuador (Formerly USNM 6668, no longer there).

Range: Upper Amazonian region of Colombia and Ecuador.

Leimadophis reginae reginae Linnaeus

Coluber reginae Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 219.—"Indiis" (RMS, 2 cotypes).

Liophis reginae quadrilineata Jan, 1863, Arch. per la Zool., vol. 2 (2), p. 84.—Ecuador; Central America; Colombia (MonM and VM; PM cotype no longer existent.)

Range: Northern South America, east of the Andes.

Leimadophis simonsi Boulenger

Philodryas simonsii Boulenger, 1900, Ann. Mag. Nat. Hist., ser. 7, vol. 6, p. 185.—Cajamarca, Peru, 9000 ft. (BM 1946.1.4.98).

Range: Peru; Ecuador.

Leimadophis taeniurus taeniurus Tschudi

Liophis taeniurus Tschudi, 1845, Arch. für Naturg., vol. 11 (1), p. 166. —"In der heissen Waldregion," Peru (VM?).

Range: Ecuador; Peru.

Leimadophis typhlus Linnaeus

Coluber typhlus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 218.—"Indiis" (RMS).

Xenodon isolepis Cope, 1869, Proc. Amer. Philos. Soc., vol. 11, p. 155.—Pebas, "Ecuador"—actually in Peru (Type not located at ANSP).

Range: South America from Argentina and Uruguay north through Guianas and Colombia.

LEPTODEIRA

1. Usually one preocular; no dark, well-defined lateral spots lying between the ovoid dorsal blotches.... *annulata annulata*
   Usually two preoculars; distinct lateral spots that lie between the lateral ends of the dorsal spots.....2

2. No nape stripe.... *septentrionalis ornata*
   A dark nape stripe that expands anteriorly to form a butterfly-shaped mark on the posttemporals and the postparietals.... *septentrionalis larcorum*

Leptodeira annulata annulata Linnaeus

Coluber annulatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 224.—"America," restricted to the Lower Amazon, Para, Brazil (ZIU 9).

Eteirodipsas wieneri Savage, 1884, Bull. Soc. Philom. Paris, ser. 7, vol. 8, p. 146.—Ecuador (type unknown).

Leptodeira nycthemera Werner, 1901, Verh. Zool.-Bot. Ges. Wien, vol. 51, p. 598.—Ecuador (BerM 16596).

Range: Amazonian Basin up to 1000 meters on eastern slopes of Ecuador, Peru and Bolivia; along Atlantic coast to São Paulo, Brazil.

Leptodeira septentrionalis ornata Bocourt

Comastes ornatus Bocourt, 1884, Bull. Soc. Philom. Paris, ser. 7, vol. 8, p. 141.—Isthmus of Darien, Panamá (PM 6201, 2 syntypes).

Range: Chocó region of Central and northwestern South America, in Costa Rica, Panamá, Colombia and Ecuador.

Leptodeira septentrionalis larcorum Schmidt and Walker

Leptodeira larcorum Schmidt and Walker, 1943, Zool. Ser. Field Mus. Nat. Hist., vol. 24, p. 311.—Chiclin, Libertad, Peru (CNHM 24302, male).

Range: Coastal regions of northern Peru and southern Ecuador; also recorded from the Upper Marañon Valley, Peru. Intergrades with *ornata* in a broad zone in the arid Pacific coastal zone of Ecuador.

LEPTOMICRURUS

Leptomicrurus narduccii Jan

Elaps narducci Jan, 1863, Arch. per la Zool., Anat., Phys., vol. 2, p. 222.—Unknown.

Elaps melanotus Peters, 1881, Sitzber. Gesell. Naturf. Freunde, Berlin, p. 51.—Sarayacu, Ecuador (BerM 9812, 2 syntypes).

Elaps scutiventris Cope, 1869, Proc. Amer. Philos. Soc., vol. 9 (82), p. 156.—Pebas, "Ecuador", actually in Peru (ANSP 6801, location of other types unknown).

Range: Amazonian slopes of the Andes of Ecuador, Peru, and Bolivia; Amazonian Brazil.

LEPTOPHIS

1. Loreal present....*depressirostris*
   Loreal absent 2
2. Ventrals 133-149; adults with a color pattern of dark oblique bands; keels present on the scales of all dorsal rows....*riveti*
   Ventrals usually more than 149; adults not with a color pattern of dark oblique bands; no keels on scales of first row of dorsals..... 3
3. Dorsum with strong coppery tint, ventrals also coppery, but slightly darker with dark brown and white streaking....*cupreus*
   Dorsum not as above, usually green or bluish, ventral color contrasts with dorsal color....*ahaetulla* subsp[4]..... 4
4. Head plates rarely margined with black; if narrow black margin is present, head plates are never marked with numerous small black spots or with a prominent large black spot on each parietal and supraocular shield....*a. occidentalis*
   Head plates margined with black and with numerous small, black spots or with a prominent large black spot on each parietal and supraocular plate 5
5. Head plates and dorsal scales with numerous small, irregularly shaped black spots, also present on extreme outer edge of ventrals anteriorly ....*a. bocourti*
   Head plates and dorsal scales not marked as above, but with a prominent large spot on each parietal and supraocular plate....*a. nigromarginatus*

Leptophis cupreus Cope

Thrasops cupreus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 106.—Napo and Marañon, Ecuador (formerly USNM 6666, now lost).

Range: Lower Amazonian slopes in Ecuador.

[4] This key is ineffective on many Ecuadorian specimens, and it is suggested that identification be made on the basis of the stated ranges of the individual subspecies until such a time as sufficient material is available to analyze more completely the situation in Ecuador (see Oliver, Bull. Amer. Mus. Nat. Hist., vol. 92, pp. 157-280, 1948).

Leptophis depressirostris Cope

Philothamnus depressirostris Cope, 1861, Proc. Acad. Nat. Sci. Philadelphia, 1860 (1861), p. 557.—Cocuyas de Veraguas, New Grenada; actually in Panamá (ANSP 5207).

Range: Atlantic slopes of Nicaragua, Costa Rica and Panamá; Pacific slopes of Colombia and Ecuador. A questionable record from Peru.

Leptophis ahaetulla bocourti Boulenger

Leptophis bocourti Boulenger, 1898, Proc. Zool. Soc. London, p. 116.—Paramba (BM 1946.1.6.67-68); and Cachabé, Ecuador (BM 1946.1.6. 76).

Range: Northwestern Ecuador and Gorgona Island, Colombia.

Leptophis ahaetulla nigromarginatus Günther

Ahaetulla nigromarginata Günther, 1866, Ann. Mag. Nat. Hist., ser. 3, vol. 18, p. 28.—Upper Amazons (BM 1946.1.4.7).

Range: Extreme southeastern Colombia, western Brazil, eastern Ecuador, and eastern Peru.

Leptophis ahaetulla occidentalis Günther

Ahaetulla occidentalis Günther, 1859, Proc. Zool. Soc. London, p. 412.—Guayaquil (BM 1946.1.4.48, male); and western Ecuador (BM 1946. 1.6.62, male).

Range: Costa Rica to western Colombia and Ecuador.

Leptophis riveti Despax

Leptophis riveti Despax, 1910, Bull. Mus. Hist. Nat. Paris, 1910, p. 368.—Gualaquiza, Ecuador, 730 m. (PM 06.259).

Range: Higher altitudes up to 5000 feet on both sides of the Andes in Ecuador; Amazonian Peru; western and north-central Colombia; Panamá. A single record from Trinidad.

LEPTOTYPHLOPS

1. Brown, lighter beneath, each scale with lighter outer edges, forming more or less distinct longitudinal lines; forehead, lips, and end of tail usually white. . . . *albifrons albifrons*

   Violet black, except for naso-labials and lower half of rostral, which are dark brown, and the first 3 pairs of lower labials, which are yellowish white. . . . *anthracinus*

Leptotyphlops albifrons albifrons Wagler

Stenostoma albifrons Wagler, 1824, *in* Spix, Serp. Brazil, ssp. nov., p. 68, pl. 25, fig. 3.—near Para, Brazil (MunM).

Range: Argentina and Paraguay to Venezuela and the Guianas.

Leptotyphlops anthracinus Bailey

Leptotyphlops anthracinus Bailey, 1946, Occ. Pap. Mus. Zool. Univ. Mich., no. 492, p. 1.—near Baños, Ecuador, 1800 meters (UMMZ 90816, male).

Range: Known only from the type locality and Abitagua, Ecuador.

LIOPHIS

1. Scales in 17 rows 2
   Scales in 19 rows.... *festae*
2. Dorsum crossbanded, no striping on body or tail..... 3
   Dorsum unicolor, or with striping on part of body and tail..... 4
3. Six or seven upper labials, third and fourth in eye.... *breviceps*
   Eight upper labials, fourth and fifth in eye.... *cobella*
4. Lateral dark streak on posterior portion of body and tail only; no lateral light streak, subcaudals less than 75.... *purpurans*
   A lateral light streak on body from head on 5th or 6th scale row, subcaudals more than 80..... 5
5. Whitish stripe on first scale row, head whitish to occiput, sides of ventrals brown, no dark streak through eye.... *albiceps*
   No whitish stripe on first scale row, dorsum of head brown, ends of ventrals yellowish white, dark streak through eye.... *subocularis*

Liophis albiceps Amaral

Rhadinaea albiceps Amaral, 1924, Jour. Washington Acad. Sci., vol. 14 (9), p. 200.—"Probably from Ecuador" (USNM 22446).

Range: Known only from the type specimen.

Liophis breviceps Cope

Liophis breviceps Cope, 1861, Proc. Acad. Nat. Sci. Philadelphia, 1860 (1861), p. 252.—Surinam (ANSP 3967).

Range: Dutch Guiana and eastern Ecuador.

Liophis cobella Linnaeus

Coluber cobella Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 218.—"America" (ZIU, no number, 2 cotypes and MAF, 1 cotype, no number).

Range: Northern South America east of the Andes.

Liophis festae Peracca

Rhadinaea festae Peracca, 1897, Bol. Mus. Torino, vol. 12 (300), p. 16.—Valley of Río Santiago, Ecuador (TurM, male).

Range: Known only from the type locality.

Liophis purpurans Duméril, Bibron, and Duméril

Ablabes purpurans Duméril, Bibron and Duméril, 1854, Erp. Gen., vol. 7 (1), p. 312.—Mana, Cayenne (PM 518).

Rhadinaea chrysostoma Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 104.—From the Napo or Marañon, Ecuador (USNM 6665).

Range: Guianas; Upper Amazons of Peru, Ecuador, and Colombia.

Liophis subocularis Boulenger

Rhadinaea subocularis Boulenger, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 9, p. 56.—Paramba, Ecuador, 3500 feet (BM 1946.1.5.81-82).

Range: Western Ecuador.

LIOTYPHLOPS

Liotyphlops petersii Boulenger

Helminthophis petersii Boulenger, 1889, Ann. Mag. Nat. Hist., ser. 6, vol. 4, p. 360.—Guayaquil, Ecuador (BM 1946.1.11.26).

Range: Northwestern Ecuador.

LYGOPHIS

1. Scales in 17 rows at midbody 2
   Scales in 19 rows at midbody . . . . *lineatus*

2. Dorsum almost unicolor light brown, with a vague lateral light line which is poorly distinguished from other dorsolateral color; vertebral black line never prominent; often with a light, dark-edged ocellus on each side of the nape . . . . *whymperi*
   Dorsal ground color brown, with the light lateral line rather strongly contrasted with dorsal color; vertebral black line prominent, at least posteriorly; usually no clearly marked light, dark-edged ocellus on each side of the nape . . . . *boursieri*

Lygophis boursieri Jan

Dromicus boursieri Jan, 1867, Icon. Gen., livr. 25, pl. II, fig. 2.—Quito, Ecuador (PM?).

Range: Río Pastaza region on Amazonian slopes of Ecuador.

Lygophis lineatus lineatus Linnaeus

Coluber lineatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 221.—"Asia." (DroM).

Range: Northern South America.

Lygophis whymperi Boulenger

Coronella whymperi Boulenger, 1882, Ann. Mag. Nat. Hist., ser. 5, vol. 9, p. 460.—Milligalli, Ecuador (BM 1946.1.4.4-5).

Liophis atahuallpae Steindachner, 1901, Anz. Akad. Wiss. Wien, vol. 38, p. 105, pl. 1, figs. 4, 4a.—Las Palmas, W. Spur of the Andes between Babahoyo and Guaranda, W. Ecuador, 2500 meters (Type no. 68 in Prince Bayern's collection, now in VM?).

Range: Western slopes of the Andes in Ecuador, above 1000 meters.

MICRURUS [5]

1. Black rings not in triads 2
   Black rings in well-defined groups of three, these "triads" separated by red zones 8

2. A contrasting band across parietals 3
   Top of head black, usually covering most of parietals, with or without a narrow light band across snout 4

3. Very narrow white (yellow?) band across parietals, does not touch frontal; dorsal pattern without red in adults, but with black rings of alternating widths .... *a. annellatus*
   A broad red band across parietals, usually across posterior tip of frontal; dorsal pattern with red rings .... *mipartitus*

4. Red zones usually much wider than black .... *c. transandinus*
   Red zones, if distinguishable, about equal in length to black 5

5. Yellow rings not distinguishable from red rings; or, yellow rings reduced to spots (i.e., to half-scales adjacent to the black rings) 6
   Yellow rings continuous .... *mertensi*

6. More than 40 black bands on the body .... *ornatissimus*
   Less than 36 black bands on the body 7

7. Subcaudals more than 30 .... *langsdorffi*
   Subcaudals less than 25 .... *spixi obscurus*

8. Anal plate entire .... *hemprichi ortoni*
   Anal plate divided 9

9. Head with a narrow light crossband on snout which may not be complete across dorsum of snout, but is indicated by yellow on lips and post-nasal area; a broader light band across parietals 10
   No crossband on snout; parietal crossband present or absent 12

10. Ventrals less than 215 .... *tschudii olssoni*
    Ventrals more than 220 11

11. A moderately slender species; ventrals 220-263; triads of black rings 8-14 .... *lemniscatus*
    Body very slender; ventrals 266-321; triads 11-20 .... *filiformis*

[5] *Elaps alienus* Werner, described from "Venezuela or Ecuador," has been shown by Schmidt (Zool. Ser. Field Mus. Nat. Hist., vol. 20, p. 212, 1936) to be a subspecies of the Central American species *Micrurus affinis* Jan.

12. Head with black pileus; a narrow light post-parietal band broadened on the temporals and posterior labials.... *e. ecuadorianus*
Head variously colored; if black the scales are sharply outlined with light 13

13. Top of head light, the upper head scales all sharply outlined with black; frontal shield very narrow.... *s. surinamensis*
Top of head not light, with dark bordered head shields; frontal normal in shape 14

14. Yellow rings very wide, as wide as outer black rings of the triads; top of head dark, the shields with light outlines.... *spixi obscurus*
Yellow rings narrower above than outer black rings of triads; head light anteriorly, with black spots.... *ancoralis ancoralis*

Micrurus ancoralis ancoralis Jan

Elaps maregravii ancoralis Jan, 1872, Icon. Gen. Ophidiens, vol. 42, pl. 4, fig. 2.—Ecuador (MunM).
Elaps rosenbergii Boulenger, 1898, Proc. Zool. Soc. London, p. 117, pl. 13.—Paramba, Ecuador (BM 1946.1.23.74, female).
Range: Pacific drainage of Ecuador.

Micrurus annellatus annellatus Peters

Elaps annellatus Peters, 1871, Monatsb. Akad. Wiss. Berlin, p. 402.—Pozuzo, Peru (BerM 7185).
Range: Amazonian lowlands of Ecuador, Peru, and Bolivia.

Micrurus carinicaudus transandinus Schmidt

Micrurus transandinus Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., vol. 20 (19), p. 195.—Andagoya, Chocó, Colombia (MCZ 32744, male).
Range: The Chocó region west of the Andes from the Gulf of Uraba to Ecuador.

Micrurus ecuadorianus ecuadorianus Schmidt

Micrurus ecuadorianus Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., vol. 20 (19), p. 196.—Río Daule, Ecuador (MCZ 3559, male).
Range: Pacific lowlands of Ecuador.

Micrurus filiformis Günther

Elaps filiformis Günther, 1859, Proc. Zool. Soc. London, p. 86, pl. 18, fig. B.—Para, Brazil (BM 1946.1.20.13).
Range: Amazonian basin of Brazil, Ecuador, and Colombia.

Micrurus hemprichi ortoni Schmidt

Micrurus hemprichi ortoni Schmidt, 1953, Fieldiana-Zoology, vol. 34, p. 166.—Pebas, Peru (MCZ 12423, male).
Range: Upper Amazon Basin in Peru and Ecuador; a single

specimen from Belem which may have been transported from the upper river.

Micrurus langsdorffii Wagler

Micrurus langsdorffi Wagler, 1824, *in* Spix, Serp. Brazil, p. 10, pl. 2, fig. 2.—Río Japura, Amazonas (Type unknown).

Elaps batesii Günther, 1868, Ann. Mag. Nat. Hist., ser. 4, vol. 1, p. 428.—Pebas, "Ecuador." This type locality is not actually Ecuadorian, as Pebas is in Peru (BM 1946.1.17.21).

Elaps imperator Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 110.—Napo and Marañon, Ecuador (ANSP 6793).

Elaps steindachneri Werner, 1901, Verh. Zool.-Bot. Ges. Wien, vol. 51, p. 599.—Ecuador (VM).

Elaps fasslii Werner, 1927, Sitzber. Akad. Wiss. Wien, vol. 135, p. 191.—Ecuador (VM—this is the same specimen that served as the type of *Elaps steindachneri*).

Range: Amazon Basin.

Micrurus lemniscatus Linnaeus

Coluber lemniscatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 224.—"Asia." (RMS, 2 cotypes). The type locality has been restricted to Belem, Para, Brazil (Schmidt and Walker, Zool. Ser., Field Mus. Nat. Hist., vol. 24, p. 294, 1943).

Range: Amazon Basin.

Micrurus mertensi Schmidt

Micrurus mertensi Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., vol. 20 (19), p. 192.—Pacasmayo, Peru (Senck 94206, male).

Range: Coastal areas of northwestern Peru and southwestern Ecuador.

Micrurus mipartitus mipartitus Duméril, Bibron, and Duméril

Elaps mipartitus Duméril, Bibron, and Duméril, 1854, Erp. Gen., vol. 7 (2), p. 1220.—Río Sucio, Colombia (The type is no longer in PM).

Elaps semipartitus Jan, 1858, Rev. Mag. Zool., p. 516.—Cayenne (MilM; the specimen in the PM is now missing).

Elaps fraseri Boulenger, 1896, Cat. Snakes Brit. Mus., vol. 3, p. 432, pl. 22.—West Ecuador (BM 1946.1.17.34).

Elaps mentalis Boulenger, 1896, Cat. Snakes Brit. Mus., vol. 3, p. 432, pl. 22.—Pallatanga, Ecuador (BM 1946.1.17.16), and Cali, Colombia (BM 1946.1.17.27).

Elaps calamus Boulenger, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 9, p. 57.—San Javier, Ecuador (BM 1946.1.20.25).

Elaps aequicinctus Werner, 1903, Zool. Anz., vol. 26, p. 249.—Venezuela or Ecuador (IRB).

Range: Darien, Panamá to western Ecuador.

Micrurus ornatissimus Jan

Elaps ornatissimus Jan, 1858, Rev. Mag. Zool., p. 521.—Mexico (MilM). Type locality in error, restricted to Río Putomayo, Colombia, by Schmidt (Fieldiana-Zoology, vol. 34, p. 345, 1955).

Elaps buckleyi Boulenger, 1896, Cat. Snakes Brit. Mus., vol. 3, p. 416, pl. 22, fig. 1.—Para, Brazil (BM 1946.1.17.18); and Canelos, Ecuador (BM 1946.1.17.17).

Range: Region of headwaters of the Amazon, from the Río Caqueta in Colombia to Southern Peru.

Micrurus spixi obscurus Jan

Elaps corallinus var. *obscura* Jan, 1872, Icon. Gen. Ophidiens, livr. 41, pl. 6, fig. 3.—Lima, Peru (Type unknown). Type locality in error, designated as Iquitos, Peru, by Schmidt (Fieldiana-Zoology, vol. 34, p. 175, 1953).

Elaps heterozonus Peters, 1881, Sitzber. Ges. Naturf. Freunde, Berlin, p. 52.—Sarayacu, Ecuador (BerM 9813).

Range: Amazonian drainage of Colombia, Ecuador, Peru, and Bolivia; head waters of Orinoco in Venezuela.

Micrurus surinamensis surinamensis Cuvier

Elaps surinamensis Cuvier, 1817, Règne Animal, vol. 2, p. 84.—Surinam (PM 4629).

Range: Guianas, periphery of Amazon Basin, Colombia, Ecuador, Peru, Bolivia and Brazil.

Micrurus tschudii olssoni Schmidt and Schmidt

Micrurus olssoni Schmidt and Schmidt, 1925, Zool. Ser. Field Mus. Nat. Hist., vol. 12 (10), p. 130, pl. 11.—Negritos, Piura, Peru (CNHM 5724, male).

Range: Pacific coastal region of NW Peru and SW Ecuador.

NINIA

1. 19 scale rows, head scales smooth. . . . *atrata*
   21 scale rows, striated head scales, short snout with high loreal. . . . *hudsoni*

Ninia atrata Hallowell

Coluber atratus Hallowell, 1845, Proc. Acad. Nat. Sci. Philadelphia, p. 245.—Within 200 miles of Caracas, Venezuela (ANSP 3410-12).

Streptophorus sebae schmidti Jan, 1862, Arch. Zool. Anat., vol. 2, fasc. 1, p. 27.—Guayaquil, Ecuador (HM).

Ninia spilogaster Peters, 1881, Sitzber. Ges. Naturf. Freunde, Berlin, p. 49.—Ecuador (Type not located in BerM).

Range: Venezuela; Colombia; Ecuador; Panamá; Costa Rica; Trinidad.

Ninia hudsoni Parker

Ninia hudsoni Parker, 1940, Ann. Mag. Nat. Hist., ser. 11, vol. 5, p. 270. —New River, British Guiana (BM 1939.1.19, male).

Range: British Guiana; Ecuador.

NOTHOPSIS

Nothopsis rugosus Cope

Nothopsis rugosus Cope, 1871, Proc. Acad. Nat. Sci. Philadelphia, vol. 2, p. 201, pl. 13, figs. 1-7.—Isthmus of Darien, Panamá (USNM 12427). *Nothopsis affinis* Boulenger, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 453.—Salidero, Ecuador (BM 1946.1.15.62, male).

Range: Atlantic coast of Nicaragua, Costa Rica, and Panamá; Pacific coast of Colombia and Ecuador.

OXYBELIS

1. Snout three times as long as eye; anal divided 2
   Snout less than three times as long as eye; anal entire 3
2. Distinct white stripe on ends of ventrals .... *fulgidus*
   No white stripe on ends of ventrals .... *a. aeneus*
3. Broad black stripe on outer ends of ventrals; lateral and vertebral brown stripe, chin very dark, spotted with black and brown ... *argenteus*
   Unicolor brown, chin lighter brown .... *brevirostris*

Oxybelis aeneus aeneus Wagler

Dryinus aeneus Wagler, 1824, *in* Spix, Serp. Brasil, p. 12, pl. 3.—Teffe, Amazonas, Brazil, according to Bogert and Oliver (Bull. Amer. Mus. Nat. Hist., vol. 83, p. 389, 1945) (MunM).

Coluber acuminatus Wied, 1885, Beitr. Naturg. Brazil, vol. 1, p. 322.—Unknown.

Range: Guatemala to southeastern Brazil.

Oxybelis argenteus Daudin

Coluber argenteus Daudin, 1803, Hist. Nat. Rept., vol. 6, p. 336.—No type locality given in description (Type not located in PM).

Range: Amazonian South America.

Oxybelis brevirostris Cope

Dryophis brevirostris Cope, 1861, Proc. Acad. Nat. Sci. Philadelphia, 1860 (1861), p. 555.—Veraguas, New Grenada, which is the same as Cocuyas de Veragua, Panamá (USNM 31349).

Range: Atlantic lowlands of Central America; Pacific lowlands of Colombia and Ecuador.

Oxybelis fulgidus Daudin

Coluber fulgidus Daudin, 1803, Hist. Nat. Rept., vol. 6, p. 352, pl. 80.—"Port au Prince, Santo Domingo"—probably in error (PM).

Range: Northern South America east of the Andes; Central America and Mexico.

OXYRHOPUS

1. Preocular either in contact with frontal or narrowly separated from it ....*petola*
   Preocular fairly widely separated from frontal by supraocular.....2
2. Head dark or mottled above.....3
   Head uniform yellow or orange....*formosus*
3. Red or pale reddish brown, dotted with blackish brown, anterior part of body may or may not have a few black cross bands disposed in threes ...*melanogenys*
   Dorsum yellow with irregular dark brown markings which may cover only a single scale or be confluent into blotches or zig-zag lines.... *fitzingeri frizzelli*

Oxyrhopus fitzingeri frizzelli Schmidt and Walker

Oxyrhopus fitzingeri frizzelli Schmidt and Walker, 1943, Zool. Ser. Field Mus. Nat. Hist., vol. 24, p. 313.—Negritos, Piura, Peru (CNHM 35997, male).

Range: Dry Pacific lowlands of Ecuador and Peru.

Oxyrhopus formosus Wied

Coluber formosus Wied, 1820, Reise in Brazil, part I, p. 257, footnote—Morro d'Arana, Brazil (type?).

Range: Amazonian South America.

Oxyrhopus melanogenys Tschudi

Sphenocephalus melanogenys Tschudi, 1845, Arch. für Naturg., vol. 11 (1), p. 163.—Peru (type?).

Range: Upper Amazonian parts of Bolivia; Peru; Brazil; and Ecuador.

Oxyrhopus petola Linnaeus

Coluber petola, Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 225.—"in Africa" (ZIU).

Range: Amazonian South America; west coast of Ecuador and Colombia; Central America. Roze (Bol. Mus. Cient. Nat., Caracas, vol. 1, p. 190, 1957) has revived the name *semifasciatus* Tschudi for the Amazonian population of this species, and it is certainly applicable to the Ecuadorian material on

the Amazonian slope. Use of this name would require action concerning names for other populations, however, elsewhere in Ecuador, and these names are not currently available.

PELAMIS

Pelamis platurus Linnaeus

Anguis platura Linnaeus 1766, Syst. Nat., 12th ed., vol. 1, p. 391.—"Surinami" (type unknown).

Range: Pacific and Indian oceans.

PHILODRYAS

1. Smooth scales; uniform green above, yellowish green below; scale rows 15 or 13 near anus.... *viridissima*
   Keeled scales; typically with darker dorsal band bounded below by lighter one, and with darker sides, yellow spotted with brown or gray ventrally; may occasionally be uniform in coloration; scale rows 17 near anus.... *elegans rufidorsata*

Philodryas elegans rufidorsata Günther

Dromicus rufidorsatus Günther, 1858, Cat. Colubrid. Snakes British Museum, p. 130.—"America," restricted to northern coastal Peru by Schmidt and Walker (BM 1946.1.9.28 and 1946.1.9.31, cotypes).

Tachymenis canilatus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, p. 104.—Guayaquil, Ecuador (USNM 12351).

Range: Pacific Lowlands of Ecuador and Peru, in drier parts.

Philodryas viridissima Linnaeus

Coluber viridissimus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 226.—"Surinami" (Unknown).

Range: Amazonian South America from Argentina to Guianas.

PLIOCERCUS

Pliocercus euryzona euryzona Cope

Pliocercus euryzonus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, p. 72.—Region of the Truando, New Grenada, which is now Colombia (Type formerly USNM 4303, now apparently lost).

Range: Colombia; Ecuador; Equatorial Brazil; Panamá.

PSEUDOBOA

Pseudoboa coronata Schneider

Pseudoboa coronatus Schneider, 1801, Hist. Amphib., vol. 2, p. 286.—"America." (Type unknown).

Range: Guianas; Brazil; Colombia; Ecuador; Peru; Bolivia.

PSEUSTES

1. Two postoculars; two anterior temporals 2
   Three postoculars; one anterior temporal. . . . *sulphureus sulphureus*
2. Dorsum unicolor, a dull brown in adults; a series of brown bands on light brown ground color, in juveniles. . . . *poecilonotus polylepis*
   Dorsum irregularly barred with yellow or each scale has a yellow center with a black edge. . . . *shropshirei*

Pseustes poecilonotus polylepis Peters

Ahaetulla polylepis Peters, 1867, Monatsb. Akad. Wiss. Berlin, p. 709.—"Surinam" (BerM 5899).

Range: Guianas; Colombia; Ecuador; Peru; Bolivia; Brazil; and Trinidad.

Pseustes shropshirei Barbour and Amaral

Phrynonax shropshirei Barbour and Amaral, 1924, Occ. Pap. Boston Soc. Nat. Hist., vol. 5, p. 131.—Fort Sherman, Canal Zone, Panamá (MCZ 18819).

Range: Costa Rica; Panamá; Pacific Colombia and Ecuador.

Pseustes sulphureus sulphureus Wagler

Natrix sulphurea Wagler, 1824, *in* Spix, Serp. Brasil, p. 26, pl. 9.—Río Japura, Brazil (MonM?).

Range: Peru; Ecuador; Brazil; Guianas; Trinidad.

RHADINAEA

1. Dorsals reduce to 15 posteriorly; subcaudals less than 75. . . . *brevirostris*
   Dorsals 17 at anus; subcaudals more than 75 2
2. Head and nape reddish; body practically unicolor, usually with a vague lighter yellow area on first scale rows above a black stripe on tips of ventrals and first scale row. . . . *pachyura fulviceps*
   Body with two or more white lines, head and nape blackish, a light spot on parietal. . . . *l. lateristriga*

Rhadinaea brevirostris Peters

Dromicus brevirostris Peters, 1863, Monatsb. Akad. Wiss. Berlin, p. 280.—Apparently from Quito, Ecuador, purchased—probably erroneous (BerM 3869).

Dromicus viperinus Günther, 1868, Ann. Mag. Nat. Hist., ser. 4, vol. 1, p. 418.—Pebas, "Ecuador," actually Peru (BM 1946.1.1.9-10).

Range: Guianas to Bolivia.

Rhadinaea lateristriga lateristriga Berthold

Liophis lateristriga Berthold, 1859, Göttingen Gelehrte Anz., vol. 3, p. 180.—Popayan, Colombia (GottM).

Dromicus frenatus Peters, 1863, Monatsb. Akad. Wiss. Berlin, p. 218.—Guayaquil, Ecuador (BerM 2126).

Urotheca coronata Steindachner, 1901, Anz. Akad. Wiss. Vienna, p. 106, pl. 1, figs. 3, 3a.—Region of Babahoyo, Ecuador (Prince Bayern Coll. no. 58).

Erythrolamprus labialis Werner, 1909, Mitt. Naturh. Mus. Hamburg, vol. 26, p. 237.—Ecuador (HM 117).

Range: Central Colombia to Ecuador on Pacific slope.

Rhadinaea pachyura fulviceps Cope

Rhadinaea fulviceps Cope, 1885, Proc. Amer. Philos. Soc., vol. 23, p. 279.—"Panamá" (USNM 14118).

Range: Panamá; Pacific Colombia and Ecuador.

RHINOBOTHRYUM

Rhinobothryum bovallii Andersson

Rhinobothrium bovallii Andersson, 1916, Meddel. Goteborg's Mus. Zool., Afd. 9, p. 32, fig. 4.—Siquirres, Costa Rica (GothM 1221).

Range: Costa Rica, Panamá, Colombia, and northwestern Ecuador, in the Chocó area.

SIBON

1. Ventrals less than 150 . . . . *dunni*
   Ventrals more than 155 2

2. Dorsal pattern often obscured by heavy deposition of black pigment, belly heavily spotted with dark brown, and may be completely black . . . . *nebulata leucomelas*
   Dorsal pattern of chocolate or reddish-brown blotches, contrasting strongly with the light brown or grayish interblotch areas . . . . *nebulata nebulata*

Sibon dunni Peters

Sibon dunni Peters, 1957, Copeia, p. 110.—Pimanpiro, San Nicholas, Imbabura, Ecuador (UMMZ 92068, male).

Range: Known only from the type locality.

Sibon nebulata nebulata Linnaeus

Coluber nebulatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 464.—"America" (RMS).

Range: Mexico to northern Brazil and Amazonian Ecuador; Trinidad; Tobago. An isolated population exists in Pacific Ecuador, south of the range of *S. n. leucomelas*.

Sibon nebulata leucomelas Boulenger

Leptognathus leucomelas Boulenger, 1896, Ann. Mag. Nat. Hist., ser. 6, vol. 17, p. 18.—Buenaventura, Colombia (BM 1895.11.16.16, female).

Range: Panamá-Colombia border through Chocó of Colombia to northwestern Ecuador.

SPILOTES

Spilotes pullatus pullatus Linnaeus

Coluber pullatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 225.—"Asia" (RMS).

Spilotes megalolepis Günther, 1865, Ann. Mag. Nat. Hist., ser. 3, vol. 15, p. 93.—South America-purchased (BM 1946.1.13.2).

Range: Central America south of Nicaragua; northern South America; Trinidad; Tobago.

STENORHINA

Stenorhina degenhardtii degenhardtii Berthold

Calamaria degenhardtii Berthold, 1846, Abh. Ges. Wiss. Göttingen, vol. 3, p. 8, tab. 1, figs. 3-4.—"New Grenada" (GottM).

Range: Central America; Pacific Colombia and Ecuador.

SYNOPHIS

1. Scales in 19 rows.... *miops*
   Scales in 21 rows.... *lasallei*

Synophis lasallei Niceforo-Maria

Diaphorolepis lasallei Niceforo-Maria, 1950, Rev. Acad. Colomb. Ciencias Exactas, etc., vol. 7 (28), p. 517, 3 figs.—Paraje situado al norte de Albán, Cundinamarca, Cordillera Oriental (vertiente occidental), 2200 m., about 60 km. NW of Bogotá, Colombia (IdlS, male).

Range: Known from type locality and from Río Sandalias, Napo-Pastaza Province, Ecuador.

Synophis miops Boulenger

Synophis miops Boulenger, 1898, Proc. Zool. Soc. London, p. 115.—Paramba, Ecuador (BM 1946.1.12.30, female).

Range: Known from type only.

TANTILLA

1. Subcaudals more than 75.... *longifrontalis*
   Subcaudals less than 75 2

2. Body with narrow (two scale rows) black half rings.... *supracincta*
   Body striped or unicolor 3

3. Tip of snout white, prefrontals contact labials..... 4
   Tip of snout dark brown, prefrontals and labials not in contact.... *melanocephala melanocephala*

4. All scales above second row brownish, below second row entirely white *melanocephala capistrata*

Dorsum striped with dark brown, light brown and white, first row of dorsal scales white on lower half. . . . *fraseri*

Tantilla fraseri Günther

Homalocranium melanocephalum fraseri Günther, 1895, Biol. Centr.-Am., Rept., fasc. 19, 1895, p. 148.—Quito, Ecuador (BM 1946.1.9.43-44), and "w. Ecuador" (BM 1946.1.8.77; 1946.1.8.80; 1946.1.9.84).

Range: High western slopes of Andes, perhaps in Quito valley.

Tantilla longifrontalis Boulenger

Homalocranium longifrontale Boulenger, 1896, Ann. Mag. Nat. Hist., ser. 6, vol. 17, p. 17.—Cali, Colombia (BM 1946.1.8.84).

Range: Eastern slopes of Andes, at lower altitudes, in Colombia and Ecuador.

Tantilla melanocephala melanocephala Linnaeus

Coluber melanocephalus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 218.—"America" (RMS).

Range: Central America throughout South America north of Argentina and east of the Andes.

Tantilla melanocephala capistrata Cope

Tantilla capistrata Cope, 1876, Jour. Acad. Nat. Sci. Philadelphia, (n. s.) vol. 8 (2), p. 181.—Valley of Jequetepeque, (Libertad), Peru (Type formerly in ANSP, now apparently lost).

Range: Northern coastal Peru to arid valley of the Marañon and the Catamayo and Malacatos Valley in southern Ecuador.

Tantilla supracincta Peters

Homalocranion supracinctum Peters, 1863, Monatsb. Akad. Wiss. Berlin, 1863, p. 272.—Guayaquil, Ecuador (BerM 4791).

Range: Ecuador, probably on coastal plain from Guayaquil northward.

THAMNODYNASTES

**Thamnodynastes pallidus* Linnaeus

Coluber pallidus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 221.—"in Indiis" (DroM).

Range: Guianas; Brazil; Peru.

Thamnodynastes nattereri Mikan

Coluber nattereri Mikan, 1820, Delect. Faun. Flor. Braz., fig. 1.—"Lectus prope Sebastianopolim."

Range: Coastal Ecuador and Peru.
Remarks: This species has been recorded from Guayaquil on the basis of USNM 12277, which Walker (Bull. Mus. Comp. Zool. Harvard, vol. 96 (1), p. 14, 1945) called *Dryophylax nattereri.*

TRACHYBOA

1. Top of head without horns.... *gularis*
   Top of head, canthus rostralis with horns.... *boulengeri*

Trachyboa boulengeri Peracca

Trachyboa boulengeri Peracca, 1910, Annular. Mus. Zool. Univ. Napoli, vol. 3 (12), p. 1.—Type locality unknown (UNZM).
Range: Chocó region of Ecuador, Colombia and Panamá.

Trachyboa gularis Peters

Trachyboa gularis Peters, 1860, Monatsb. Akad. Wiss. Berlin, p. 200, fig. 1.—Guayaquil, Ecuador (BerM 3770-71, 2 syntypes).
Trachyboa gularis multimaculata Rosen, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 15, p. 169.—Balao, Ecuador (LunM).
Range: Dry parts of western coastal Ecuador (Brazil?).

TRETANORHINUS

Tretanorhinus taeniatus Boulenger

Tretanorhinus taeniatus Boulenger, 1903, Ann. Mag. Nat. Hist., ser. 7, vol. 12, p. 350.—Río Sapayo, N. W. Ecuador, 450 feet (BM 1946.1.15. 40).
Range: Pacific coast in Colombia and Ecuador.

TRIPANURGOS

Tripanurgos compressus Daudin

Coluber compressus Daudin, 1803, Hist. Nat. Rept., vol. 6, p. 247.—Surinam (PM 3730).
Range: Brazil; Paraguay; Bolivia; Colombia; Ecuador; Guianas; Trinidad; Panamá.

TROPIDOPHIS

1. Smooth scales; 200 ventrals, 42 subcaudals, 11 upper labials with 3 entering eye.... *battersbyi*
   Keeled scales, 150-160 ventrals, 25-31 subcaudals, 8-9 upper labials with 2 entering eye.... *taczanowskyi*

Tropidophis battersbyi Laurent

Tropidophis battersbyi Laurent, 1949, Bull. Inst. Roy. Sci. Nat. Belg., vol. 25 (9), p. 6.—"Equateur" (IB 739-I.G. no. 3701).

Range: Known only from the type specimen.

Tropidophis taczanowskyi Steindachner

Ungalia taczanowskyi Steindachner, 1880, Sitzber. Akad. Wiss. Wien, vol. 80, Abt. 1, p. 522.—Tambillo, Peru (VM 2 cotypes).

Range: Amazonian Peru and Ecuador; Brazil?.

TYPHLOPS

Typhlops reticulata Linnaeus

Anguis reticulatus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 228.—"America" (Type unknown).

Range: Guianas; Venezuela; Brazil; Ecuador; Colombia; Peru; Argentina; Trinidad.

XENODON

1. Anal entire; scales in 19 rows (rarely 21) . . . . *rhabdocephalus*
   Anal divided; scales in 21 rows . . . . *severus*

Xenodon rhabdocephalus Wied

Coluber rhabdocephalus Wied, 1825, Beitr. Naturges. Brasil, vol. 1, p. 351.—Sertão von Bahia (Type unknown).

Range: Central America; Colombia; Ecuador; Bolivia; Brazil.

Xenodon severus Linnaeus

Coluber severus Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 219.—"Asia" (RMS).

Range: Amazonian South America.

XENOPHOLIS

Xenopholis scalaris Wucherer

Elapomorphus scalaris Wucherer, 1861, Proc. Zool. Soc. London, p. 235.—Cañaviera, Matta de S. João, Bahia, Brazil (BM 1946.1.8.60, cotype; other cotypes?).

Range: Brazil; Bolivia; Ecuador.

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